

ANATOMY AND RELATIONSHIPS OF THE PAREIASAUR *PAREIASUCHUS NASICORNIS* FROM THE UPPER PERMIAN OF ZAMBIA

by M. S. Y. LEE, C. E. GOW and J. W. KITCHING

ABSTRACT. A well-preserved and newly prepared skull has enabled a critical re-evaluation of the genus *Pareiasuchus* (Reptilia; Pareiasauridae) and the species *Pareiasuchus uasicornis*. The skull is heavily ossified, deeply sculptured, akinetic and anapsid. The skull roof sutures are described for the first time. Most elements typical of basal amniotes are present; however, the postparietal is a single median ossification, the tabular is absent, and a 'supernumerary element' (possibly a modified cervical osteoderm) is present. Among the better-known pareiasaur taxa, *Pareiasuchus* appears to be most closely related to *Pareiasaurus*, *Scutosaurus* and *Elginia* – other forms with highly elaborate cranial ornament. Autapomorphies of *Pareiasuchus* include: forked distal end of humerus; and proximal end of femoral shaft greatly bent preaxially. Autapomorphies of *P. uasicornis* include: posteriorly projecting cheek flanges; medially inflected premaxillary and maxillary teeth; and a discrete ossification over each external naris. The specimen demonstrates that many features previously suggested to be unique (amongst basal amniotes) to procolophonoids and turtles also characterize pareiasaurs: for instance, wide antorbital buttress formed by the prefrontal and palatine; short cultriform process; and medially enclosed adductor fossa. *P. uasicornis* was a large terrestrial herbivore, as evidenced by the crenulated, labiolingually flattened tooth crowns, depressed jaw articulation, small gape, heavy jaws, reduced transverse flange of the pterygoid, and heavy, akinetic skull. The distinctive cheek flange and angular boss were probably defensive structures.

PAREIASUCHUS uasicornis Houghton and Boonstra, 1929a is one of the most common and distinctive pareiasaurs. Although several complete skulls are known, its cranial anatomy has yet to be adequately described and interpreted. Indeed, the only previous description of the cranium of this taxon is a short paragraph, three photographs of the holotype, and some rough sketches where all the sutures are hypothetical (Boonstra 1934a). The postcranial anatomy, however, has been studied more adequately, and appears to be indistinguishable from that of *Pareiasuchus peringueyi* (Boonstra 1929a, 1929b, 1932, 1934b, 1934c; Houghton and Boonstra 1930).

Recently, a well-preserved skull of a sub-adult *Pareiasuchus uasicornis* has been prepared at the Bernard Price Institute of Palaeontology, Johannesburg. This specimen is unusual in that it shows clearly all the external cranial sutures, which are not yet known in *Pareiasuchus uasicornis* and very poorly known in most other pareiasaurs. A description of this skull should therefore not only fill a gap in our knowledge of the anatomy of *Pareiasuchus uasicornis*, but also shed light on the systematic position of *Pareiasuchus uasicornis* within pareiasaurs, and of pareiasaurs within amniotes in general. Recent debate on the last topic (Gauthier *et al.* 1988b; Lee 1993, 1995; Laurin and Reisz 1995) has been hampered by the absence of a good description of even a single pareiasaur. Finally, functional aspects of the highly distinctive pareiasaur skull are discussed.

Institutional Abbreviations. BPI, Bernard Price Institute for Palaeontological Research, Johannesburg, South Africa; GSP, Geological Survey, Pretoria, South Africa; PIN, Palaeontological Museum of the Russian Academy of Sciences, Moscow, Russia; SAM, South African Museum, Cape Town, South Africa; WEL, Welwood Museum, Graaff-Reinet, South Africa.

SYSTEMATIC PALAEONTOLOGY

Remarks. Following recent arguments (e.g. de Queiroz and Gauthier 1992), higher taxa have not been assigned formal Linnean ranks. Rigorous definitions and diagnoses of Amniota, Reptilia, and Pareiasauria are provided in, respectively, Gauthier *et al.* (1988a, 1988b), Laurin and Reisz (1995) and Lee (1995).

AMNIOTA Haeckel, 1866
REPTILIA Laurenti, 1768
PAREIASAURIA Seeley, 1888

Genus PAREIASUCHUS Broom and Haughton, 1913

Type species. *Pareiasuchus periugueyi*.

Diagnosis. A moderate-sized pareiasaur, reaching 2 m in snout-vent length, possessing a highly rugose skull, and deep cheek flanges with large pointed bosses on the posterior and ventral edges. Osteoderms are present over the entire dorsum and limbs: most of these are isolated, but some are suturally united. By analogy with *Elginia* (see Maxwell 1991), the compound osteoderms presumably covered the shoulder and pelvic regions.

Pareiasuchus is characterized by numerous unique postcranial specializations (autapomorphies) not found in other pareiasaurs: the ent- and ectepicondyles are both narrow and project *distally*, the distal end of the humerus therefore appearing 'forked'; the iliac shaft is greatly inclined anterodorsally, more so than in any other pareiasaur; the second and third sacral ribs are greatly flattened, appearing almost sheet-like; and the proximal end of the femoral shaft is greatly bent preaxially, the femur therefore appearing boomerang-shaped in dorsal or ventral aspect. There are two species, *P. peringueyi* and *P. nasicornis*.

Remarks. Haughton and Boonstra's (1929, p. 86) original diagnosis of *Pareiasuchus* was as follows: 'snout rounded. Cheek deep and rugose. Ilium as in *Pareiasaurus*. Ischium long'. This diagnosis is not very adequate, as none of these traits is unique to *Pareiasuchus*, nor is the combination of all these traits unique. Indeed, all four traits occur in most pareiasaurs. However, the genus *Pareiasuchus* is monophyletic and can be diagnosed via the other features mentioned above.

Pareiasuchus nasicornis Haughton and Boonstra, 1929a

Plate 1; Text-figures 1-8

- 1929a *Pareiasuchus nasicornis* Haughton and Boonstra, p. 86.
1929b *Pareiasuchus nasicornis* Haughton and Boonstra; p. 263, pl. 36.
1929a *Pareiasuchus nasicornis* H. and B.; Boonstra, p. 99.
1930 *Pareiasuchus nasicornis* H. and B.; Haughton and Boonstra, pp. 312, 337, fig. 52.
1932 *Pareiasuchus nasicornis* H. and B.; Boonstra, pp. 442, 447, 479-481.
1933 *Pareiasuchus nasicornis* H. and B.; Hartmann-Weinberg, p. 45.
1934a *Pareiasuchus nasicornis* H. and B.; Boonstra, pp. 8, 23, 33, pls 1-3.
1934b *Pareiasuchus nasicornis* H. and B.; Boonstra, pp. 44, 48, pl. 27.
1934c *Pareiasuchus nasicornis* H. and B.; Boonstra, p. 61.
1937 *Pareiasuchus nasicornis* H. and B.; Hartmann-Weinberg, p. 684.
1940 *Pareiasuchus nasicornis* H. and B.; Broom, p. 158.
1944 *Pareiasuchus nasicornis* H. and B.; von Huene, p. 399.
1969 *Pareiasuchus nasicornis* H. and B.; Kuhn, p. 66, fig. 36; p. 78, fig. 39-7.
1977 *Pareiasuchus nasicornis* H. and B.; Kitching, pp. 55, 68-69.
1984 *Pareiasuchus nasicornis* H. and B.; Araújo, pp. 235, 249.

- 1987 *Pareiasuchus nasicornis* H. and B.; Ivachnenko, p. 78.
 1989 *Pareiasuchus nasicornis* H. and B.; Araújo, p. 307.

Holotype. SAM 3016: complete skull and lower jaw; parts of both forelimbs, pelvis, and both hindlimbs; numerous osteoderms.

Type locality and horizon. Graaff-Reinet Commonage, South Africa; *Cistecephalus* Zone, Upper Permian (Kitching 1977).

Referred specimens. BPI 1/254: skull fragment and partial lower jaw. BPI 1/1500: antorbital region of skull, with mandible missing part of left ramus. BPI 1/3653: complete skull and lower jaw; unprepared blocks containing anterior cervicals, osteoderms and portions of (?) shoulder girdle. GSP 475: complete skull and lower jaw; posterior 3 sacra and anterior caudals; portions of shoulder and pelvic girdles. GSP CBT4: skull missing most of roof; complete lower jaw. GSP R320: pelvis; portions of both forelimbs and both hindlimbs; 17 caudals; ribs and osteoderms. GSP TN257: complete skull and lower jaw. SAM K6607: complete skull with lower jaw; unprepared postcranial blocks containing vertebrae, parts of pelvis and hindlimb, and osteoderms. All except BPI 1/3653 are from the *Cistecephalus* Zone of South Africa. BPI 1/3653 (described here) is from the *Cistecephalus* Zone of Zambia.

Diagnosis. Based on previously studied specimens, *P. nasicornis* differs from the very similar *P. peringueyi* in lacking the two autapomorphies for that taxon: the blunt angular boss, and long posteriorly directed spine on the palatal ramus of the quadrate (Haughton and Boonstra 1929*b*; Lee in press). It also possesses at least two autapomorphies of its own: the large descending cheek flanges project backwards, making the skull appear 'delta-shaped' in dorsal aspect; and the marginal teeth in the upper jaw point inwards towards the palate. In all other pareiasaurs (including *P. peringueyi*), the large cheek flanges, when present, project laterally. In most other pareiasaurs (including *Pareiasuchus peringueyi*) the marginal teeth in the upper jaw point directly downwards. However, inflected marginal teeth occur in one other pareiasaur, *Bradysaurus baini*. The present study (see below) has revealed two other autapomorphies of *P. nasicornis*: the anteriorly directed boss over the external nostril is a discrete ossification, not an extension of the nasal bone; and the cultriform process is shorter and wider than in all other pareiasaurs.

Remarks. *P. nasicornis* might possess two other autapomorphies. In the femur of adults (SAM 3016 and GSP R320), the internal trochanter extends distally all the way to the preaxial tibial facet. However, this condition does not occur in a juvenile (SAM K6607), where the internal trochanter fades out along the shaft of the femur, the condition found in all other pareiasaurs including *P. peringueyi*. As befits its name, *P. nasicornis* possesses distinct, anteriorly directed bosses over the external nares, close to the skull midline (Haughton and Boonstra 1929*a*). These are poorly developed in *P. peringueyi*. However, among other pareiasaurs, the bosses are also well-developed in a few individuals of *Scutosaurus* (Ivachnenko 1987). They are also well-developed in *Elginia*, but are located further laterally, away from the skull midline (Newton 1893; Walker 1973; Maxwell 1991). The distinct, sagittally located bosses over the nares in *P. nasicornis* are probably autapomorphic for this species, occurring convergently in the other two taxa, but this interpretation must remain tentative.

Haughton and Boonstra (1929*a*), followed by Boonstra (1934*a*), suggested that *Pareiasuchus nasicornis* further differed from *P. peringueyi* in possessing smaller bosses on the skull roof and cheek, and a shorter palate. However, there appear to be no clear-cut differences in these areas. The bosses are weakly developed in juveniles of both *Pareiasuchus nasicornis* (e.g. GSP TN257) and *P. peringueyi* (e.g. WEL RC784), and are prominent in adults. The palate is of similar shape in both species. Haughton and Boonstra (1929*a*) suggested that the angular boss in *P. nasicornis* was inflected medially, unlike that in any other pareiasaur. However, this appears to be a taphonomic artefact: in their specimen (SAM 3016), the boss appears to have been bent inwards by dorso-ventral crushing.

DESCRIPTION

General

Material (Pl. 1; Text-figs 1–2). BPI 1/3653, complete skull and lower jaw; plus a small unprepared block containing disarticulated anterior cervicals, osteoderms and portions of shoulder girdle. As discussed above, the postcranial anatomy of *P. nasicornis* has already been described, and this work will therefore concentrate on the cranium.

Locality. Northern (Chikonta) Group, Locality 21 of Kitching (1963), Upper Luangwa Valley, Zambia (formerly Northern Rhodesia).

Horizon. Lowermost *Cistecephalus* Zone. The genus *Cistecephalus* occurs at locality 21 as isolated specimens together with abundant small and some medium-sized dicynodonts (Drysdall and Kitching 1963; Kitching 1963). This faunal assemblage is approximately equivalent to the original *Endothiodon* Zone of Broom (1909), renamed the *Tropidostoma-Endothiodon* Assemblage Zone by Keyser and Smith (1977). This horizon has been incorporated into the lowermost *Cistecephalus* Zone (Kitching 1970, 1977).

Identification. BPI 1/3653 can be referred to *Pareiasuchus nasicornis* on the basis of possession of all three cranial autapomorphies already known to be characteristic of that species: the backwardly projecting cheek flanges, inflected marginal teeth on the upper jaw, and prominent nasal bosses. It is identical to the type and to all other referred specimens of *P. nasicornis* in almost all other features, although each of these traits is also found in at least some other pareiasaurs. There are slight differences in the cranial ornamentation among all the skulls referred to *P. nasicornis* but, as suggested in the discussion below, these are probably ontogenetic differences.

Soft anatomy. Information on soft anatomical features associated with various osteological landmarks (foramina, grooves, etc.) is derived from Gaffney (1979, 1990) and Heaton (1979). These are the two most comprehensive published discussions of basal amniote soft anatomy. Heaton used extant diapsids as analogues for *Eocaptorhinus*, whereas Gaffney (1979, 1990) used extant turtles as analogues for extinct turtles such as *Proganochelys*. However, for all the osteological landmarks discussed in this work, the two workers reached identical conclusions regarding the associated soft anatomy, suggesting that their conclusions are general for basal amniotes, including pareiasaurs such as *Pareiasuchus*. In particular, because turtles and captorhinids form successive extant outgroups to the taxon under study, soft anatomical features common to both can be reasonably inferred to characterize *P. nasicornis* as well, unless the osteology of *P. nasicornis* suggests otherwise (Bryant and Russell 1992; Witmer 1995).

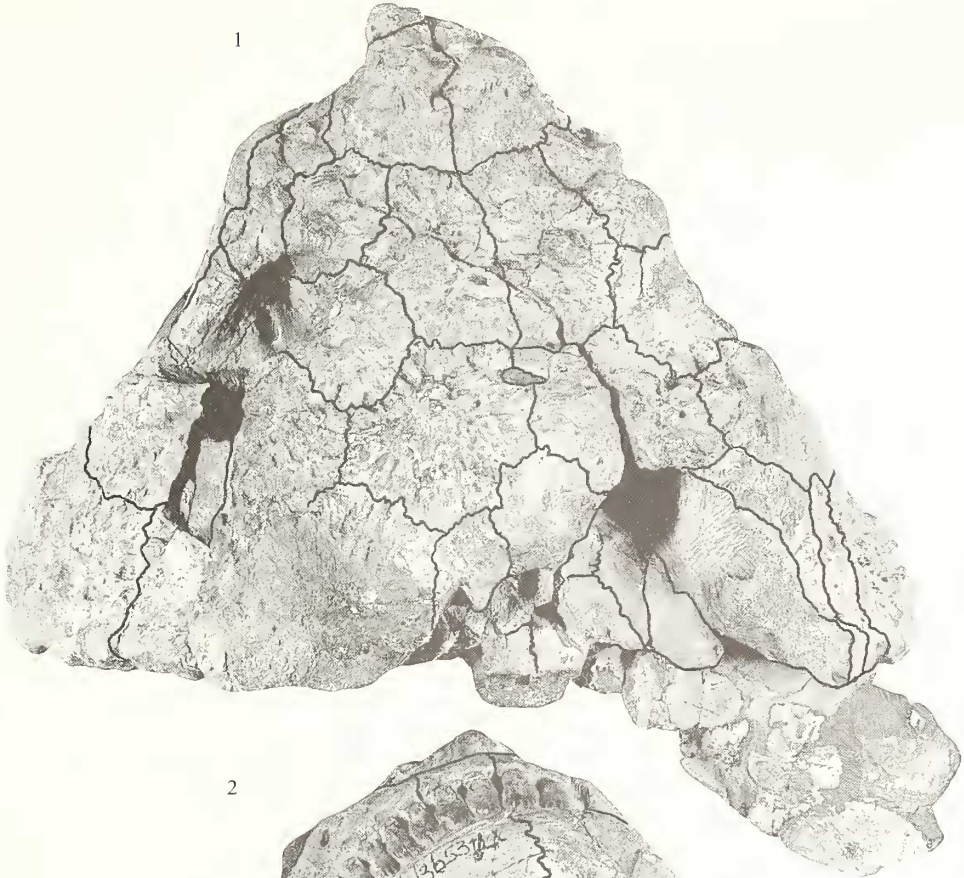
Dermal roofing elements (Pl. 1; Text-figs 1–2, 4–5)

General. The elements of the skull roof are well-preserved. The posterior part of the skull table is slightly damaged. Most of the posterior edge is weathered, and a portion on the right side is missing. Consequently, the posterior limit of the postparietal and supernumerary elements cannot be ascertained, and the dorsal margin of the posttemporal fenestra, formed by the supernumerary and supratemporal elements, is unclear. A narrow wedge-shaped strip is missing from the left cheek behind the orbit, but this region is preserved on the right side. The shape of the pineal foramen indicates that the skull table has been slightly compressed anteroposteriorly. Also, comparisons with other skulls of *P. nasicornis* (see *Referred specimens*) indicate that the right cheek is undistorted, while the left cheek has been pushed slightly forwards. This is consistent with the observation that the right cheek is undamaged whereas the left cheek has a portion missing.

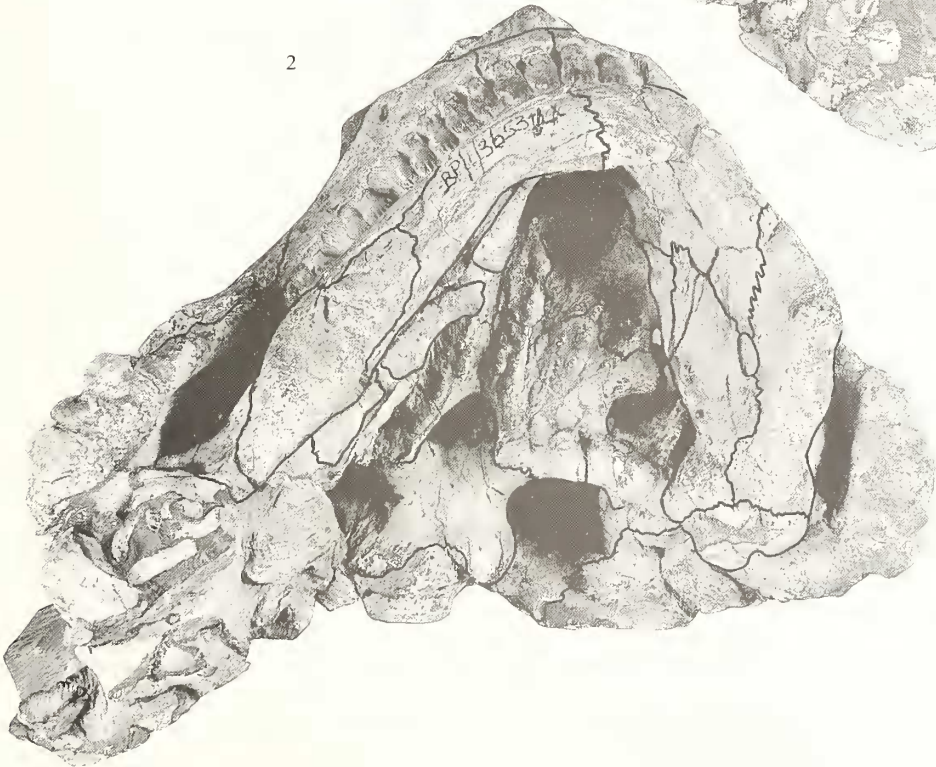
EXPLANATION OF PLATE I

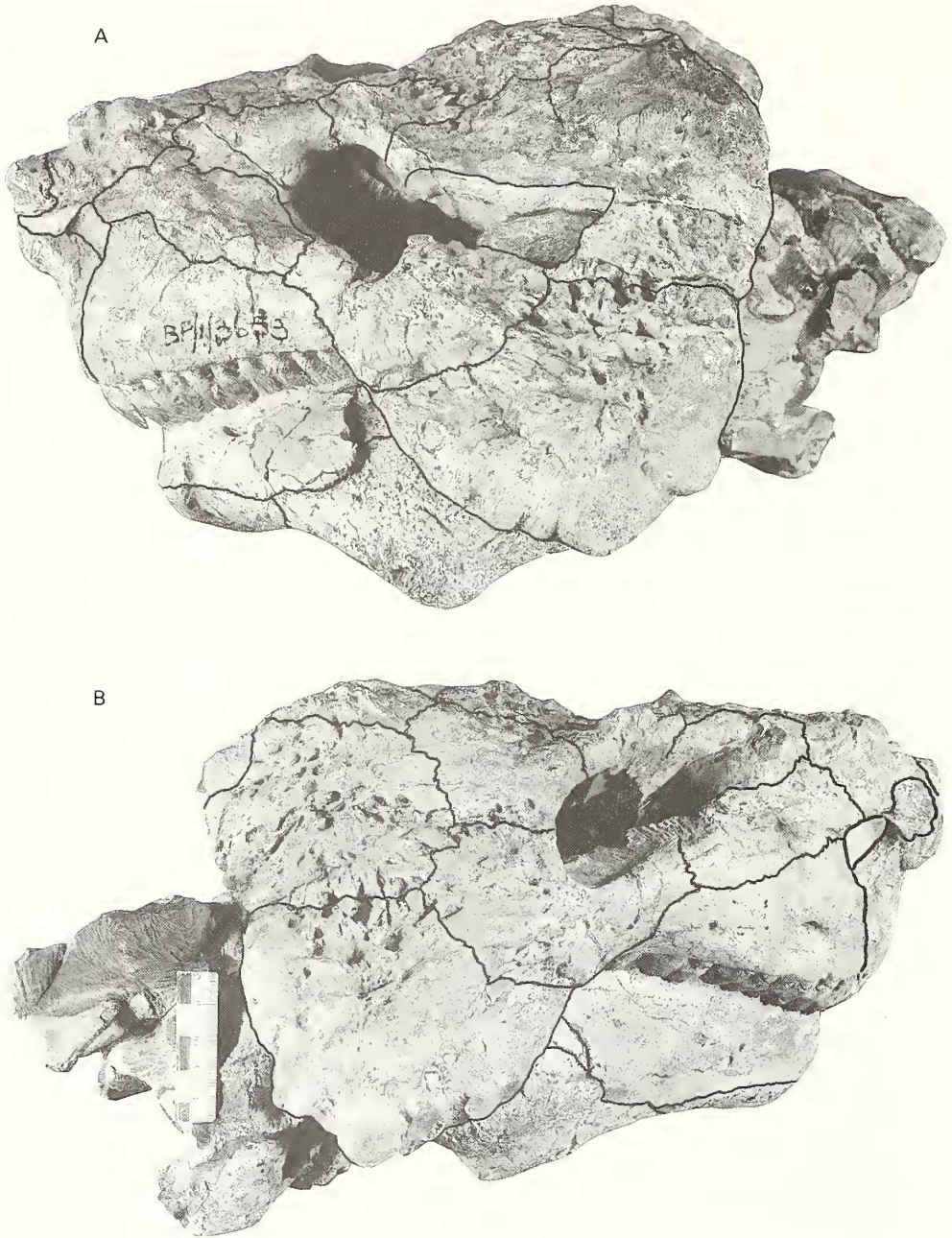
Figs 1–2. *Pareiasuchus nasicornis* Houghton and Boonstra, 1929a; BPI 1/3653; skull. 1, in dorsal view; 2, in ventral view; $\times 0.4$.

1



2

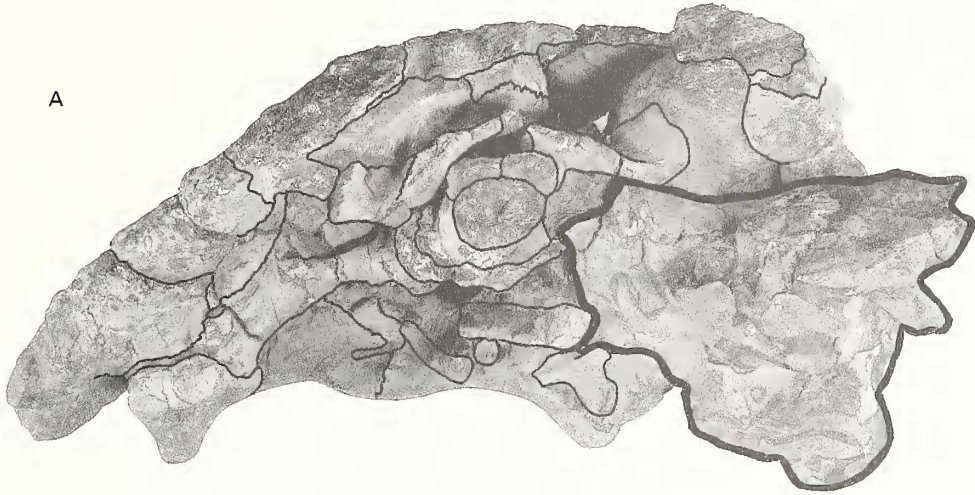




TEXT-FIG. 1. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a; BPI 1/3653; skull in A, left lateral view; B, right lateral view; $\times 0.42$.

The skull is approximately triangular in dorsal (or ventral) aspect, with a broad, rounded snout and large, posterolaterally directed cheek flanges. In lateral view, the snout is the same height along its entire length; it does not taper anteriorly. The external naris is a large, circular opening that faces anteriorly. The orbit faces laterally and is located very slightly in front of the middle of the skull. It is elongated along the anterodorsal-

posteroventral axis. The pineal foramen is located slightly behind the posterior limit of the orbit. Unusually for pareiasaurs, almost all external cranial sutures are clearly visible. Most roofing elements characteristic of basal amniotes are present. However, the postparietal is a single median ossification, and the tabular is absent (the element sometimes identified as the 'tabular' is the supratemporal: see Discussion). A supernumerary element is present between the postparietal and the supratemporal.



A



B

TEXT-FIG. 2. *Pareiasuchus nasicornis* Houghton and Boonstra, 1929a, BPI 1/3653. A, skull in posterior view; a block of unprepared postcranial fragments, outlined in a thick black border, partly obscures the right side of the specimen in this photograph; $\times 0.53$. B, view looking forwards and medially into the left orbit, showing details of the antorbital buttress; $\times 0.87$.

The external surface of each bone on the skull roof, except the premaxilla and maxilla, is heavily sculpted. Usually, one or more bosses are located near the centre of the element, and irregular, rugose ridges radiate over the rest of the external surface. Small rounded pits are present in the grooves between the ridges.

Nasal. The nasal is a quadrilateral element which tapers anteriorly and is slightly longer than wide. It sutures with its partner along the skull midline. A short groove on its external surface, near its anterior tip, receives the dorsal process of the premaxilla. The nasal also contacts the lacrimal, prefrontal, and frontal, and forms the dorsal margin of the external naris. Two bosses are present on the anterior part of each nasal. On the anterior tip of each nasal, directly above the suture with the premaxilla, there is another boss composed of a discrete ossification. This boss, and the suture, are clearly visible on the left nasal. On the right nasal, the boss is missing, and the sutural surface of the nasal is exposed.

Frontal. The frontal is an approximately rectangular element forming most of the interorbital region. Medially, it has a long suture with its partner along the skull midline. It also contacts the nasal, prefrontal, postfrontal and parietal. It does not enter the orbital margin. A prominent boss is present, located slightly towards the rear of the element.

Parietal. The parietal is a large, squarish element forming most of the posterior skull roof. It sutures with the frontal, postfrontal, postorbital, supratemporal and postparietal. Medially, it forms a long suture with its partner along the skull midline. The pineal foramen is located along this suture, about one-third of the way back from the anterior end. In all other skulls of *P. nasicornis*, the foramen is round: in this specimen anteroposterior compression has distorted it into a transverse slit. A large, rounded boss is present in the centre of the parietal.

Postparietal. The postparietal is the only unpaired element on the skull roof. It is a median, U-shaped bone that forms the centre of the posterior part of the skull table. Anteriorly, it extends into an embayment between the parietals. Laterally, it sutures with the supernumerary element. The external surface of the postparietal is covered with the usual rugae and pits; however, there is no central boss. A sagittal process on the internal (ventral) surface of the postparietal meets the dorsal process of the supraoccipital, forming a robust pillar connecting the braincase to the skull table. The posterior margin is damaged and has been reconstructed on the basis of other specimens of *P. nasicornis* (e.g. SAM 3016).

Supernumerary element. The supernumerary element is a small triangular bone wedged between the postparietal, parietal, and supratemporal. The external surface lacks a boss, but is weakly sculpted with the usual rugae and pits. The posterior margin is damaged and has been reconstructed through comparison with other specimens of *P. nasicornis* (e.g. SAM 3016). The homology of this bone is addressed in the Discussion below.

Premaxilla. The premaxilla is a small element forming the tip of the snout and the medial and ventral margins of the external naris. Medially, it sutures with its partner along the skull midline. The premaxilla also sutures with the maxilla and nasal. The palatal portion of the premaxilla is obscured by the lower jaws; however, in all other pareiasaurs, the premaxilla sutures with the vomer, and forms the anterior margin of the internal naris and the lateral and anterior margin of the single median foramen praepalatium. The premaxilla lacks dermal ornament and bears two large alveoli.

Maxilla. The maxilla is a vertical plate of bone, highest anteriorly and tapering posteriorly. Anteriorly, it forms most of the posterior margin of the external naris. It does not enter the orbital margin. On the skull roof, the maxilla sutures with the premaxilla, lacrimal, and jugal. The posterior limit of the maxilla just contacts the anterior tip of the quadratojugal, excluding the jugal from the ventral cheek margin. The entire external surface of the maxilla is unornamented. Anteriorly, there is a foramen maxillare, representing the exit for a ramus of the arteria alveolis superior. Another, smaller foramen further back along the external surface of the maxilla may represent the exit of another branch of this artery. A groove for the blood vessel extends anteriorly from each of these openings.

The ventral surface of the palatal portion of the maxilla is obscured by the articulated lower jaws in all specimens of *P. nasicornis*. However, part of the dorsal surface is visible through the orbit of BPI 1/3653 (Pl. 1, fig. 1; Text-fig. 4A). A narrow horizontal palatal ledge is present on the medial surface of the maxilla. This



TEXT-FIG. 3. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a. A, anterior view of snout, showing premaxillary and anterior maxillary teeth in labial view. The black vertical line is the skull midline suture, between the premaxillae and the dentaries; $\times 1.03$. B, lingual view of partially erupted tooth from the middle of the mandibular tooth row. Because of difficulty of access, preparation and photography of this tooth has been poor; $\times 0.94$.

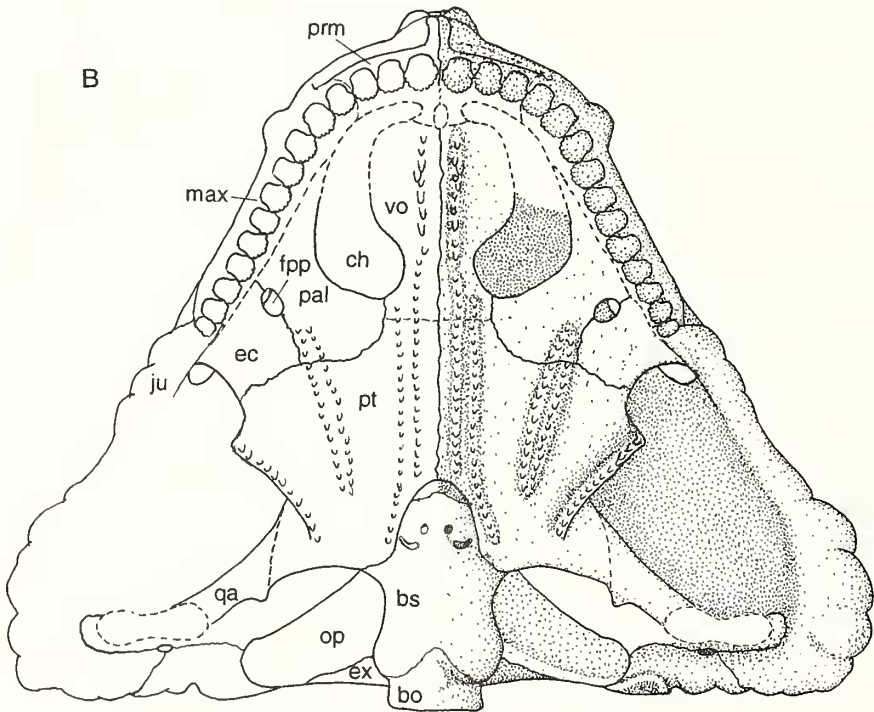
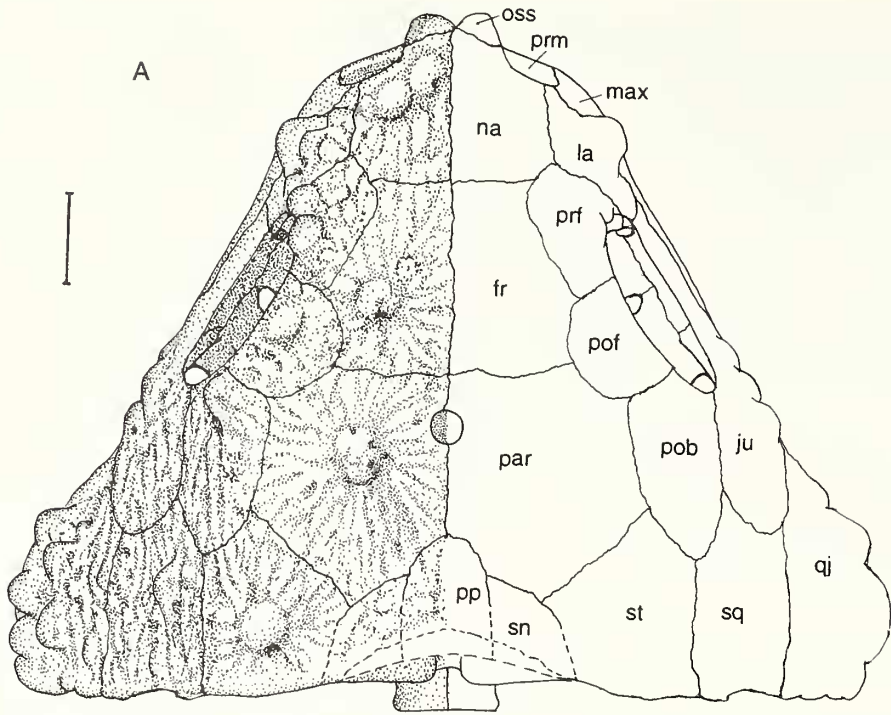
ledge sutures with the ectopterygoid and palatine. The area of the ledge in front of the orbit is obscured by the antorbital buttress. Presumably, as in all other pareiasaurs, the ledge continues anteriorly in front of the palatine and forms part of the lateral border of the internal naris.

The maxilla bears 12 alveoli, which are largest anteriorly and gradually decrease in size posteriorly. The alveolar ridge is narrow, barely wider than the tooth bases.

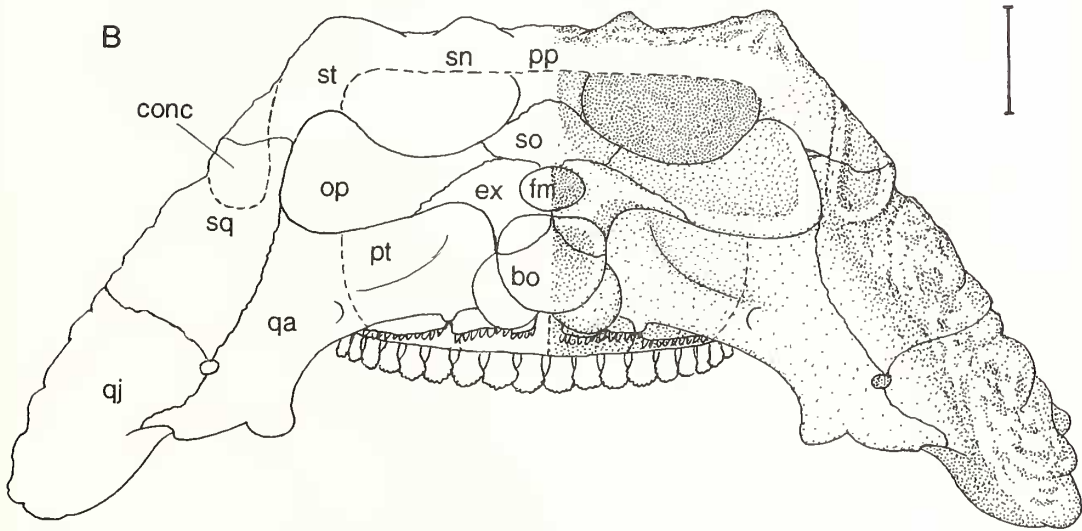
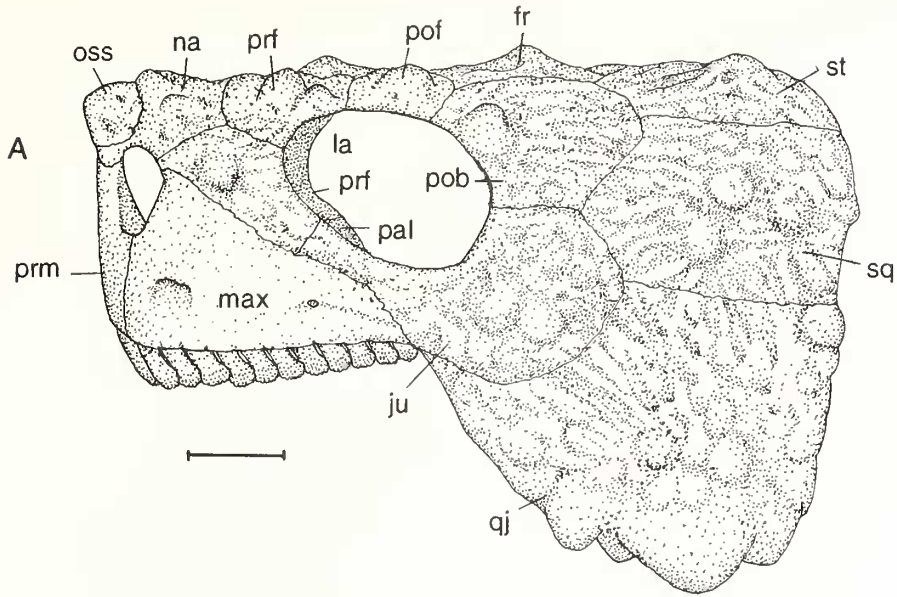
Lacrimal. The lacrimal is a long element forming much of the facial region, much of the anterior margin of the orbit and a very small portion of the margin of the external naris. It is largely excluded from the latter opening by the anterior expansion of the maxilla, and sutures with the nasal, prefrontal, maxilla and jugal. Along the orbital margin, the internal surface of the lacrimal sutures with the descending (antorbital) flange of the prefrontal. The foramen orbitonasale penetrates the base of the antorbital buttress, at the quadruple junction between the lacrimal, prefrontal, palatine and jugal. This opening between the fossa orbitalis and the fossa nasalis transmitted the palatine branch of the facial nerve (VII), the lateral ramus of the facial nerve, and the prefrontal vein. A single large rounded boss is present, located slightly towards the anterior of the element.

Prefrontal. The prefrontal consists of a curved plate which forms part of the skull roof, and an antorbital buttress. The skull roof portion is horizontal and sutures with the lacrimal, nasal, frontal, and postfrontal. Two prominent bosses are located above the orbital margin. The antorbital buttress is a curved, vertical flange (Text-fig. 5B). It is oriented anterolaterally and is narrowest dorsally, gradually widening ventrally. The medial edge is smoothly concave; the lateral edge sutures with the medial surface of the lacrimal. Ventrally, the descending flange of the prefrontal meets a dorsal flange of the palatine and forms part of the medial border of the foramen orbitonasale (see *Lacrimal*).

Postfrontal. The postfrontal is a sizeable, semicircular element which forms most of the dorsal orbital margin. It sutures with the prefrontal, frontal, parietal, and postorbital, and bears a prominent boss nears its anterolateral edge.



TEXT-FIG. 4. For caption see opposite.



TEXT-FIG. 5. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a. Reconstruction of the skull in A, left lateral, and B, occipital view. Scale bars represent 30 mm.

Postorbital. The postorbital is a curved plate, consisting of a horizontal dorsal portion, which forms part of the skull table, and a ventrolaterally oriented ventral portion, which forms part of the cheek. It forms much of the posterodorsal portion of the orbital margin, and sutures with the prefrontal, parietal, supratemporal,

TEXT-FIG. 4. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a. Reconstruction of the skull in A, dorsal, and B, ventral view. Scale bar represents 30 mm.

squamosal, and jugal. A prominent boss is present near the orbital margin, on the junction between the cheek and skull table.

Supratemporal. The supratemporal is an irregularly shaped plate which forms most of the posterior skull roof. It sutures with the parietal, supernumerary, supratemporal, squamosal, and postorbital. Most of the external surface is heavily sculpted, but this ornamentation becomes weaker near the posterior edge. There is a prominent central boss.

A ventrally directed flange is present on the medial surface of supratemporal, near the posterolateral corner. This flange meets the upturned distal end of the paroccipital process.

Squamosal. The squamosal is a flat, rectangular element that forms the posterodorsal region of the cheek. It sutures with the supratemporal, postorbital, jugal, and quadratojugal. Three prominent central bosses are present on the external surface. On the medial surface, a vertical flange sutures with the dorsal ramus of the quadrate.

The posterior edge of the squamosal forms part of the posterior margin of the cheek. Along this edge, there is a peculiar raised area of uncertain function. This area is teardrop-shaped, with the pointed end directed dorsomedially. The surface of this raised area is shallowly concave. Immediately below this structure, a narrow groove extends dorsolaterally across the posterior edge of the cheek.

Jugal. The jugal is a flat, crescent-shaped element that forms the cheek region below and behind the orbit. It forms the entire ventral margin of the orbit, and sutures with the postorbital, squamosal, quadratojugal, maxilla, and lacrimal. A central clump of bosses is present, below the posteroventral margin of the orbit. The ventral surface of the palatal portion of the jugal is obscured by the articulated lower jaw in all specimens of *P. nasicornis*. However, the dorsal surface is visible through the orbit of BPI 1/3653 (Pl. 1, fig. 1; Text-fig. 2A): there appears to be a small horizontal palatal flange which extends medially to overlap the ectopterygoid. This has been termed the 'medial process' (Gaffney and Meylan 1988; Gaffney 1990), the 'alary process' (Gauthier *et al.* 1988b), or the 'internal process' (Heaton 1979).

Quadratojugal. The quadratojugal is the largest element on the skull roof. It is a flat, quadrilateral bone that forms most of the ventral portion of the cheek. The anterior tip of the quadratojugal just manages to contact the maxilla. The quadratojugal also sutures with the jugal and squamosal.

The quadratojugal is greatly expanded ventrolaterally, far beyond the level of the tooth row. This expansion forms a large cheek plate that covers the posterior half of the lower jaw, and is the structure upon which the name 'pareiasaur' (cheek-lizard) is based (Owen 1876). The ventral corner of this cheek plate bears a very prominent conical boss, the posterior margin is thickened and adorned with several smaller bosses. Another three small bosses are present immediately in front of the large corner boss; however, further anteriorly, the edge of the cheek plate is a straight, thin, unornamented edge. This edge meets the alveolar ridge of the maxilla at an angle of about 135°.

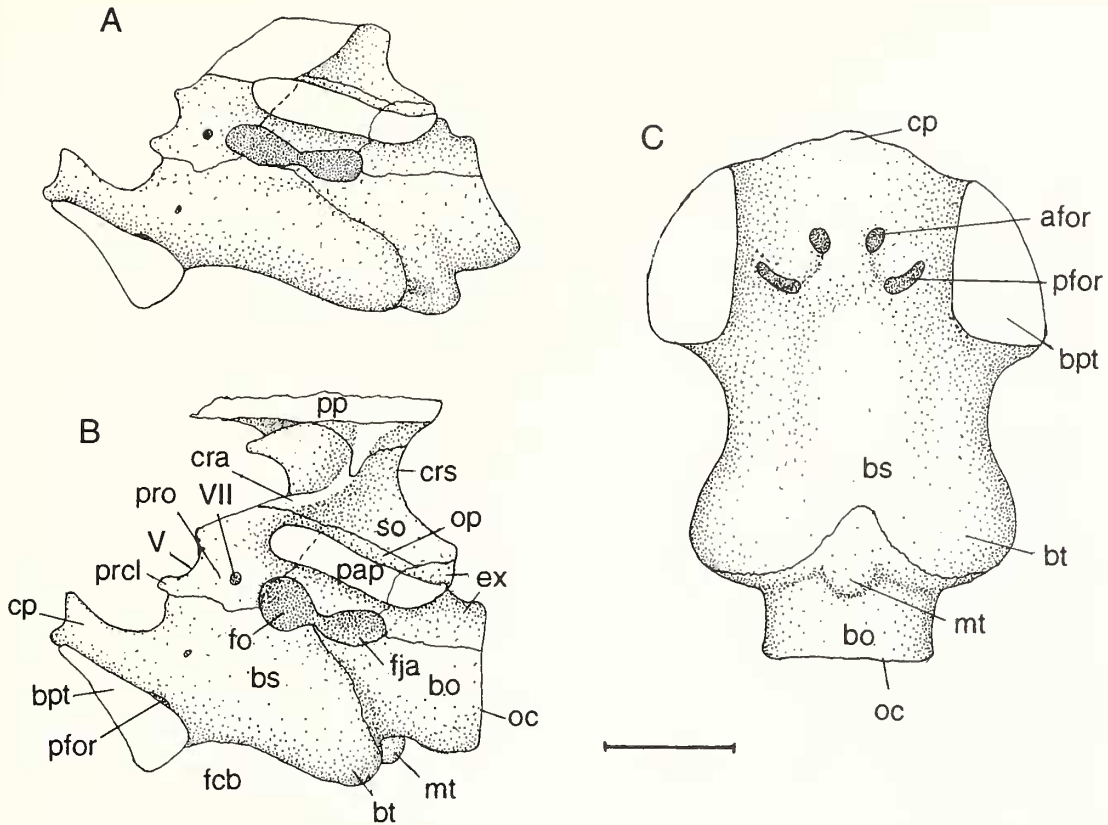
A flange extends medially from the internal surface of the quadratojugal, to meet the quadrate (Text-fig. 5B). Dorsally, this flange is continued by a similar structure on the squamosal. The quadrate foramen is located on the triple junction of the quadratojugal, squamosal, and quadrate (see *Quadrate*).

Palate, palatoquadrate and braincase (Pl. 1, fig. 2; Text-figs 2, 4B, 5B, 6)

General. The braincase and palatal elements are well-preserved, with only slight distortion. Parts of the braincase are covered by the skull roof and much of the lateral and anterior regions of the palate are obscured by the articulated lower jaws.

The basioccipital has been pushed slightly dorsally towards the skull roof, and the distal ends of both paroccipital processes have partially separated from the skull roof. The missing portion of the skull table has exposed the dorsal surface of the paroccipital process and lateral surface of the supraoccipital. The stapes is not preserved; the copula (basihyal), and the left second ceratobranchial, are present but have been displaced towards the right ramus of the lower jaw.

The palate forms a horizontal roof over the oral cavity, and is raised well above the level of the alveolar ridge. All the elements characteristic of basal amniotes are present, including the ectopterygoid. The internal naris is large, and the posterior portion is located well away from the alveolar ridge. The foramen palatinum posterius is large, and is also located well away from the alveolar ridge. A small interpterygoid vacuity is



TEXT-FIG. 6. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a. A, braincase of BPI 1/3653, in left lateral view. B, reconstruction of the braincase in left lateral view, using information derived from both sides of the specimen. The paroccipital process and the left cheek are omitted. C, reconstruction of basisphenoid and basioccipital in ventral view. Scale bar represents 20 mm.

present, and the basiptyergoid 'articulation' is sutural and completely immobile. The transverse flange of the pterygoid is weakly developed and the subtemporal fenestra is consequently extensive.

A single row of small conical denticles extends along the posterior edge of the transverse flange of the pterygoid. A double row extends anterolaterally from the interptyergoid vacuity towards the foramen palatinum posterius. Another double row extends anteriorly from the interptyergoid vacuity to the posterior margin of the internal naris. This double row continues anteriorly, medial to the internal naris, as a single row of larger denticles, and posterolaterally along the margin of the interptyergoid vacuity as a single row of small denticles.

Vomer. The vomer is a long element that forms most of the palate medial to the internal naris. Medially, it sutures with its partner along the skull midline. The anterior portion of the vomer is obscured by the articulated lower jaws in all individuals of *P. nasicornis*. Presumably, as in all other pareiasaurs, it forms the posterior border of the single median foramen praepalatinum, and contacts the palatal process of the premaxilla. The lateral edge of the vomer forms the medial margin of the internal naris. This margin is concave both anteriorly and posteriorly. The posterior limit of the vomer is unclear in all specimens of *P. nasicornis*. Presumably, as in *Scutosaurus karpinskii*, the only pareiasaur in which this suture is known (Lee 1994b), the vomer extended slightly behind the posterior limit of the internal naris, and sutured with the palatine and pterygoid.

A single, high, longitudinal ridge, bearing a row of approximately nine large conical denticles, extends along the medial margin of the vomer. This ridge is located on the anterior half of the vomer, very close to the

midline. This ridge continues posteriorly along the vomer and on to the pterygoid, as a weaker ridge with smaller denticles. Near the presumed pterygoid-vomer suture, another similar denticulated ridge begins. This ridge is positioned lateral and parallel to the previous ridge, and also continues posteriorly along the pterygoid.

Palatine. The palatine is an irregularly shaped element that forms much of the lateral region of the palate, between the internal naris and the foramen palatinum posterius. A long, tapering process extends anteriorly, between the internal naris and the maxilla. The ventral surface of the palatine-maxilla suture is obscured by the lower jaw in all specimens of *P. nasicornis*. The palatine also sutures with the ectopterygoid, pterygoid, lacrimal, and presumably the vomer (see *Vomer*). A large foramen palatinum posterius occurs in the middle of the palatine-ectopterygoid suture. This opening is oval, being slightly elongated along the suture. In turtles and squamates, this foramen is mostly filled with connective tissue, but also forms the ventral exit for branches of the nasal and maxillary arteries, and of the maxillary nerve (Gaffney 1979, 1990).

On the ventral surface, medial to the foramen palatinum posterius, two ridges extend posteriorly and slightly medially. Each bears 3 or 4 small conical denticles. Anteriorly, these ridges converge slightly; posteriorly, they continue on to the pterygoid.

On the dorsal surface of the palatine, in front of the orbit, a flange extends perpendicularly upwards to meet the descending flange of the prefrontal and enter the margin of the foramen orbitonasale (see *Prefrontal*).

Ectopterygoid. The ectopterygoid is a small rectangular element that forms the portion of the palate behind the foramen palatinum posterius. It contacts the maxilla, jugal, pterygoid, and palatine. The foramen palatinum posterius (see *Palatine*) occurs in the centre of the suture with the palatine. The ventral surface of the lateral portion of the ectopterygoid is obscured by the lower jaws in all specimens of *P. nasicornis*: however, the dorsal surface is visible through the orbit of BPI 1/3653. The posterolateral edge of the ectopterygoid is concave and forms the anterior margin of the subtemporal fenestra. The exposed area of the ventral surface of the ectopterygoid does not bear any ridges or denticles.

Pterygoid. The pterygoid is a large, complex element. Anteriorly, it sutures with the palatine and ectopterygoid. The suture with the vomer is unclear, but appears to be located at the level of the posterior margin of the palatine. Laterally, the pterygoid forms the medial border of the subtemporal fenestra. The transverse flange (processus pterygoideus externus) is weakly developed. It extends horizontally, with only a slight ventrolateral inclination, and therefore does not project ventrally below the tooth row. The posterior border of the transverse flange bears a single row of approximately 13 small conical denticles.

The pterygoids are sutured together along the anterior midline. Posteriorly, a small triangular interpterygoid vacuity is present between them. The anterior border of this vacuity is rounded. A ridge, bearing approximately 12 small conical denticles, extends anteriorly from the anterior end of the interpterygoid vacuity. Another ridge, bearing approximately 20 denticles, lies parallel and immediately lateral to it and continues posterior along the lateral margin of the interpterygoid vacuity. Both ridges continue anteriorly onto the vomer. Another pair of ridges extends anterolaterally, from the middle of the pterygoid towards the foramen palatinum posterius. Each ridge bears approximately 15 small conical denticles. Posteriorly, the ridges converge. Anteriorly, the ridges continue onto the palatine.

Behind the interpterygoid vacuity, the pterygoid forms an extensive suture with the basiptyergoid process of the basisphenoid. The plane of the sutural surface faces dorsally and slightly posteriorly and medially. The basicranial 'articulation' is therefore completely akinetic.

The quadrate ramus of the pterygoid extends posteriolaterally from the basicranial articulation, and forms most of the wall separating the temporal fossa from the middle ear. The wall is lowest medially, near the basicranial articulation. Laterally, the quadrate ramus gradually gets higher until, near the cheek, it almost reaches the paroccipital process. Further laterally, the wall is continued by the quadrate. The suture between the quadrate and pterygoid is, however, unclear in all known specimens of *P. nasicornis*, and has been restored according to the pattern found in *P. peringueyi* (BPI 1/4105).

From the ventral margin of the quadrate flange, a wide horizontal ledge extends posteriorly, partly flooring the cranioquadrate space. This ledge continues medially on to the basiptyergoid process, and laterally on to the quadrate.

Quadrate. The quadrate is a triangular, vertical plate, oriented perpendicularly to the skull midline. It forms part of the wall between the middle ear cavity and the subtemporal fossa. Medially, the quadrate contacts the quadrate flange of the pterygoid, although this suture is unclear (see *Pterygoid*). The lateral margin contacts the flange on the medial surface of squamosal and the quadratojugal. The quadrate foramen is located at the

triple junction of the quadrate, squamosal, and quadratojugal. This foramen has not been reported in turtles, but is present in captorhinids and diapsids, where it is traversed by the mandibular nerve and 'muscular artery' (Heaton 1979). The dorsal tip of the quadrate extends almost to the distal end of the paroccipital process.

From the ventrolateral corner of the quadrate, a descending process bears the articular surface for the lower jaw. This surface is obscured by the articulated lower jaws in all individuals of *P. nasicornis*. Presumably, as in other pareiasaurs, it consists of a lateral and a medial condyle, separated by a groove.

The posterior surface of the quadrate forms part of the anterior wall of the middle ear cavity. The ventral margin bears a horizontal ledge, which projects posteriorly and partially floors this cavity. This ledge bears a small tubercle and continues medially onto the pterygoid. The tubercle is not found in captorhinids or turtles, but is present in some other basal amniotes (e.g. procolophonoids). No function has yet been proposed for it, although it might have been part of the articulation with the stapes. *Proganocheilus* and captorhinids both have a pit in exactly this position, the columellar recess (Heaton 1979) or 'quadrate pocket' (Gaffney 1990), which has been interpreted to receive the distal end of the stapes.

Basisphenoid. The area occupied by the parasphenoid and basisphenoid in primitive tetrapods is occupied by a single complex ossification, here termed simply the basisphenoid, following Gaffney (1979, 1990). This element forms the anterior portion of the thick floor of the cavum cranii. Posteriorly it sutures with the basioccipital. The sutural surface is deeply concave transversely, and faces posterodorsally. Thus, the basioccipital extends under (i.e. ventral to) the basisphenoid, and forms much of the external ventral surface of the braincase. Posteriorly, two large hemispherical basal tubera occur on this surface, along the basisphenoid-basioccipital suture. On the lateral surface, the basisphenoid-basioccipital junction appears as a curved, anterodorsally oriented suture which extends to the ventral margin of the fenestra ovalis. The basisphenoid forms the anteroventral margin of the fenestra ovalis. In front of the fenestra ovalis, the basisphenoid forms the base of the lateral wall of the cavum cranii. This wall is continued dorsally by the prootic.

The basiptyergoid process projects anterolaterally from the anterior of the basisphenoid, and is firmly sutured to the pterygoid. The sutural area is very long (anteroposteriorly) and faces ventrally, and slightly anteriorly and laterally.

The basisphenoid extends anteriorly as a wide, extremely short cultriform process. It contains two foramina on the ventral surface, near the basiptyergoid process. The posterior foramen exits on the dorsal surface of the basiptyergoid process; the course of the anterior foramen is not known. These openings have not been reported in any other basal amniotes, and their former contents are uncertain.

Prootic. The prootic forms part of the anterior sidewall of the cavum cranii. Anteriorly, its dorsal margin is embayed for the trigeminal nerve, while posteroventrally it forms part of the border of the fenestra ovalis. The facial (VII) nerve exits from a small foramen in the centre of the prootic. The prootic sutures with the basisphenoid ventrally, the opisthotic posteriorly, and the supraoccipital dorsally.

Opisthotic. The opisthotic forms most of the posterior sidewall of the cavum cranii and most of the paroccipital processes. An anteroventral flange forms the posterior margin of the fenestra ovalis. Ventrally, the opisthotic forms the dorsal border of the very large foramen jugulare anterius, traversed by the vagus (X) and accessory (XI) nerves, and the vena cerebri posterior.

The fenestra ovalis and the foramen jugulare anterius are confluent, although almost separated by processes from the opisthotic and basisphenoid. Posterior to the foramen jugulare anterius, the opisthotic sutures with the exoccipital, which sends a long flange laterally along the ventroposterior surface of the paroccipital process. Dorsally, above the paroccipital process, the opisthotic sutures with the supraoccipital.

The paroccipital process is situated immediately above the fenestra ovalis and foramen jugulare anterius. It is a thick, curved plate of bone that extends posterolaterally to the cheek. The transverse axis is also slightly inclined, so that the dorsal surface faces slightly posteriorly, while the ventral surface faces slightly anteriorly. The dorsal surface is convex, and the ventral surface flat, along the anteroposterior dimension. Proximally, the paroccipital process is very broad anteroposteriorly. Distally, it gradually becomes narrower. The distal tip curves dorsally and sutures with the supratemporal and squamosal. In this specimen, however, distortion has caused the paroccipital process and the skull roof to separate slightly.

Exoccipital. The exoccipital is a small element forming the posterior region of the braincase and part of the occiput. It consists of a vertical plate, which forms the lateral wall of the posterior region of the cavum cranii and part of the occipital condyle, and a horizontal flange, which extends along the paroccipital process.

Anteriorly, the vertical plate forms the posterior border of the foramen jugulare arterius. Above this foramen, it has a horizontal suture with the opisthotic. Below this foramen it has a horizontal suture with the basioccipital. Posteriorly, it forms the lateral and ventral borders of the foramen magnum. Above the foramen magnum, the exoccipital sutures with the supraoccipital: it does not meet its partner dorsally. The foramen magnum is oval, being widest along the horizontal axis. Below the foramen magnum, the exoccipital sutures with its partner and projects posteriorly beyond the level of the foramen magnum. This portion forms the laterodorsal corner of the occipital condyle. The two exoccipitals are almost completely separated by the basioccipital, but just contact one another along the dorsal margin of the occipital condyle.

Lateral to the foramen magnum, the exoccipital sends a long triangular flange along the paroccipital process. This flange covers the proximal portion of the posterior surface of the paroccipital process, tapering distally. It also covers the ventral surface of the paroccipital process near the foramen magnum.

Basioccipital. The basioccipital forms the thick posterior floor of the cavum cranii, and most of the occipital condyle. It extends anteriorly over the dorsal surface of the basisphenoid. In lateral view, basisphenoid-basioccipital suture extends posteroventrally. In ventral view, the basioccipital-basisphenoid suture is deeply convex anteriorly: the basioccipital projects anteriorly between the basal tubera.

Dorsally, the basioccipital forms the ventral margin of the foramen jugulare arterius (see *Opisthotic*). The suture with the exoccipital extends posteriorly from the foramen to the surface of the occipital condyle.

The basioccipital forms most of the occipital condyle, except for the dorsolateral portions which are formed by the exoccipitals. The condyle is almost circular, but the dorsal edge, under the foramen magnum, is slightly flattened. The articular surface is concave, and projects a short distance behind the foramen magnum.

Supraoccipital. The supraoccipital is a thick vertical pillar. Dorsally, it sutures with the median ventral flange from the postparietal. Ventrally, the supraoccipital is expanded, forming the roof of the posterior portion of the cavum cranii. Laterally, this expansion sutures with the opisthotic, above the paroccipital process. Posteriorly, it projects between the two exoccipitals, forming the dorsal margin of the foramen magnum.

Pleurospenoid. The region of the pleurospenoid is inaccessible and this element has not been prepared. It was presumably present, as in all other pareiasaurs.

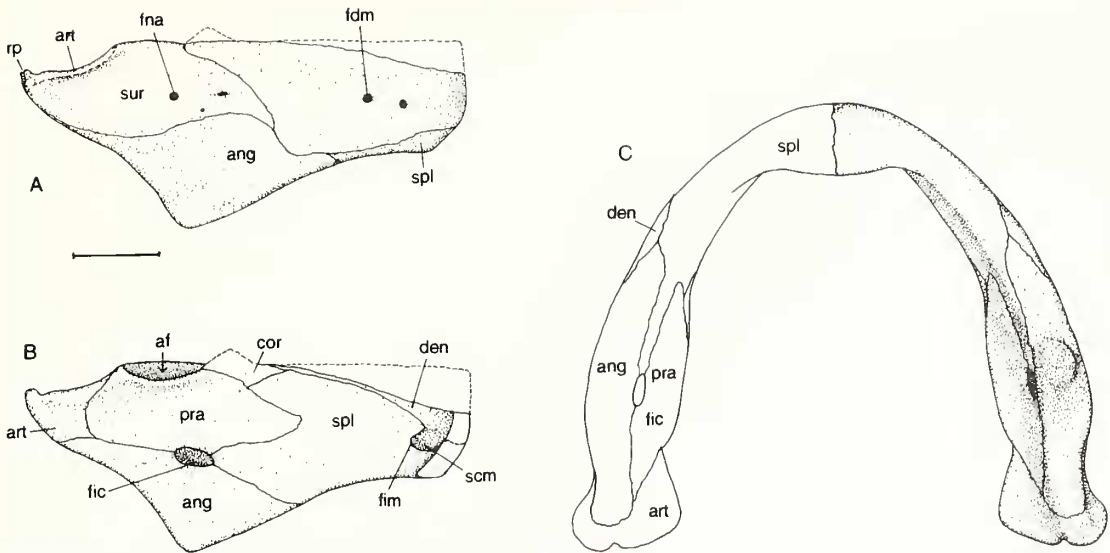
Stapes (Columella auris). The stapes is not preserved.

Hyoid apparatus. (Text-fig. 8c). The copula (basihyal) is a long, flat plate, slightly expanded at each end for articulation with the ceratobranchials. The anterior edge is firmly pressed against the lower jaw and thus not accessible to preparation. This suggests that the lingual process is absent, and that the anterior edge was most probably straight, as in all other pareiasaurs. The posterior edge is concave. The second ceratobranchial is a long bent rod, widest proximally and gradually tapering distally.

Lower jaw (Pl. 1, fig. 2; Text-figs 1, 4B, 7)

General. The lower jaw is preserved in articulation, and is complete and undistorted. However, the jaws are tightly closed, making certain areas inaccessible to preparation. All the mandibular elements characteristic of basal amniotes are present. There is only one coronoid, as in all basal amniotes except synapsids. The surfaces of the lower jaw are smooth and unsculpted. Each ramus is short and very deep. The posterior portions of the rami are straight and almost parallel, converging very slightly; anteriorly, they curve medially to meet each other and form a broad, smoothly rounded arch. The lower jaw is slightly smaller than the upper jaw, so that the labial surfaces of the mandibular teeth shear past the lingual surfaces of the maxillary and premaxillary teeth. The articular cotyle is positioned slightly below the level of the tooth row.

Dentary. The dentary forms most of the anterior portion of the lower jaw. It is exposed extensively on the lateral surface, overlapping the splenial anteroventrally, the angular posteroventrally and the surangular posterodorsally. Anteriorly, it sutures with its partner and forms the dorsal half of the symphysis. On the medial surface, the dentary is almost completely covered by the splenial: only the anterior tip, and a thin splint above the splenial, are exposed. The alveolar ridge is inaccessible to preparation. In all other pareiasaurs, the lower jaw has slightly fewer teeth than the upper jaw, and the dentary teeth decrease in size posteriorly; based on this, there were probably about 12 alveoli on the dentary, decreasing in size posteriorly.



TEXT-FIG. 7. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a. Reconstruction of the lower jaw in A, lateral view, B, medial view, C, ventral view. Scale bar represents 30 mm.

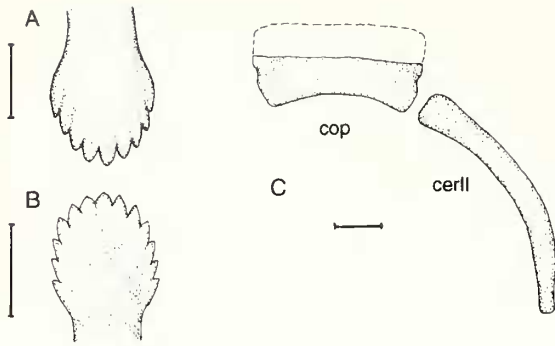
Two foramina are visible on the lateral surface of the dentary. A small unnamed opening is located half-way up the lower jaw, near the symphysis, while a slightly larger opening, the foramen dentofaciale majus, is located slightly more posteriorly and dorsally. The former contents of these foramina are, surprisingly, unknown (see Gaffney 1979). The dentary forms the dorsal wall of a groove on the medial surface of the lower jaw, the sulcus cartilaginis meckelii, occupied by part of Meckel's cartilage. This groove extends horizontally from the symphysis and leads posteriorly to the foramen intermandibularis medius, which contained Meckel's cartilage and the ramus intermandibularis medius of the mandibular (V3) nerve. The lateral edge of this foramen is formed by the dentary, the medial edge by the splenial.

Angular. The angular is mostly covered by the other elements of the lower jaw. Its greatest exposure is ventral, where it forms the posterior two-thirds of the ventral surface of the mandible. On the lateral surface, the angular is overlapped by the dentary anteriorly and by the surangular dorsally. Posteriorly, it covers the ventral surface of the articular. On the medial surface, the angular is overlapped by the splenial anteriorly and the prearticular dorsally.

The angular forms the ventral half of the border of the foramen intermandibularis caudalis, a large oval opening situated mid-way along the angular and traversed by the ramus intermandibularis caudalis of the mandibular (V3) nerve. Anterior to this foramen, on the ventral surface of the angular, there is a large rounded swelling, the 'angular boss'.

Surangular. The surangular is a sheet-like element that forms much of the lateral surface of the posterior portion of the lower jaw. It overlaps the angular ventrally, the articular posteriorly, and is overlapped by the dentary anteriorly. Its dorsal edge forms the lateral rim of the adductor fossa. In the centre of the surangular, there is a small round opening, the foramen nervi auricotemporalis. This opening is present in turtles and diapsids, where it is traversed by the ramus cutaneous recurrens (r. auricotemporalis) of the mandibular nerve (V3). The foramen is absent in captorhinids, but numerous tiny pits in this region have been interpreted as exits for a network of minute branches of this nerve (Heaton 1979). Two smaller foramina, of unknown function, are present near the anterior end of the surangular.

Articular. The articular forms the posterior portion of the lower jaw. It is overlapped ventrally by the angular, laterally by the surangular and medially by the prearticular. Only the posterior end and dorsal surface of the articular are not covered by other elements. The dorsal surface is almost horizontal, facing only very slightly outwards. This area is greatly expanded transversely, and bears the area articularis mandibularis (a.a.m.).



TEXT-FIG. 8. *Pareiasuchus nasicornis* Haughton and Boonstra, 1929a. A, reconstruction of premaxillary tooth, in labial view. B, reconstruction of partially erupted mandibular tooth, in lingual view. C, reconstruction of the preserved portions of the hyoid apparatus in ventral view. Scale bar represents 10 mm.

The a.a.m. is covered by the quadrate in this specimen; presumably, as in other pareiasaurs, it consists of two antero-posteriorly elongated cotyles separated by a low ridge. The articular projects only a very short distance behind the a.a.m., forming a very short, broad retroarticular process. The posterior end of the process is blunt and is notched in the centre.

Prearticular. The prearticular is a sheet-like element which forms much of the medial surface of the posterior end of the lower jaw. It overlaps the splenial anteriorly and overlaps the articular posteriorly. Dorsally, it overlaps the coronoid and forms the medial margin of the adductor fossa. This section of the margin curls medially, forming a prominent horizontal lip. Ventrally, the prearticular overlaps the angular and forms the dorsal margin of the foramen intermandibularis caudalis (see *Angular*).

Coronoid. The coronoid is a small bone mostly covered laterally by the dentary, and medially by the splenial and prearticular. It forms a very small portion of the anterior rim of the adductor fossa. The coronoid process is not accessible to preparation in BPI 1/3653 and is either poorly preserved or similarly inaccessible in the other specimens of *P. nasicornis*: it has been reconstructed by comparison with other pareiasaurs (e.g. *Deltavjatia vjatkensis*, PIN 2212/6).

Splenial. The splenial forms much of the medial and ventral surface of the anterior portion of the mandible. Dorsally, it overlaps the coronoid. It overlaps the dentary almost completely, leaving just a thin splint exposed immediately below the tooth row. Ventrally, the splenial overlaps the angular, curving under it to meet the dentary on the ventral surface of the mandible.

Two flanges project posteriorly from the splenial. The ventral flange is longer and enters the anterior margin of the foramen intermandibularis caudalis (see *Angular*). The dorsal flange overlaps the coronoid. Anteriorly, the splenial is deeply notched. The base of this notch forms the medial wall of the foramen intermandibularis medius (see *Dentary*). Two flanges extend anteriorly, above and below this notch. The shorter, dorsal flange terminates well before the symphysis. The longer, ventral flange forms the ventral border of the sulcus cartilaginis meckelii (see *Dentary*) and broadly sutures with its partner, forming the ventral half of the mandibular symphysis. The ventral portion of the symphysis projects posteriorly, resulting in a median ventral flange in the 'chin' area.

Marginal dentition

General (Text-fig. 2B–C). All the marginal teeth are preserved. However, as the jaws are tightly closed, the lingual surfaces of the premaxillary and maxillary teeth are inaccessible, whilst all surfaces of most of the dentary teeth are difficult to prepare. One partially erupted dentary tooth, however, is located low down on the dentary, and it has been possible to prepare most of the lingual surface of this tooth.

Upper marginal dentition (Text-figs 3A, 8A). All the premaxillary and maxillary teeth are deeply thecodont. The teeth decrease in size posteriorly, such that the posteriormost are half the dimensions of the anteriormost. They are arranged in a single row, and closely spaced so that adjacent crowns are very slightly overlapping. The dentition thus forms a continuous shearing edge. The teeth are inflected medially, so that the crowns point not directly downwards, but also inwards towards the palate.

The premaxillary and maxillary teeth are all very similar in shape. Each crown is fan-shaped, being compressed labiolingually and expanded anteroposteriorly along the jaw margin beyond the limit of the root. Nine to eleven cusps are spaced evenly around the crown. The three central cusps are slightly larger than the cusps along the anterior and posterior edges. The crown is slightly recurved, so that the apex curves slightly inwards towards the palate.

Lower marginal dentition. The only tooth exposed on the dentary (Text-figs 3B, 8B) differs in shape from all the teeth in the upper jaw. The crown is taller, there are more cusps (13), and they extend further down along the anterior and posterior margins of the crown. Also, the cusps on the anterior and posterior margins point slightly to the side of the tooth (i.e. anteriorly or posteriorly), rather than directly terminally. The crown is also not recurved lingually. Exactly the same situation occurs in *Pareiasuchus peringueyi* (BPI 1/4105) and *Scutosaurus karpinskii* (Lee 1994b): the upper and lower teeth of at least some pareiasaurs, therefore, were different.

DISCUSSION

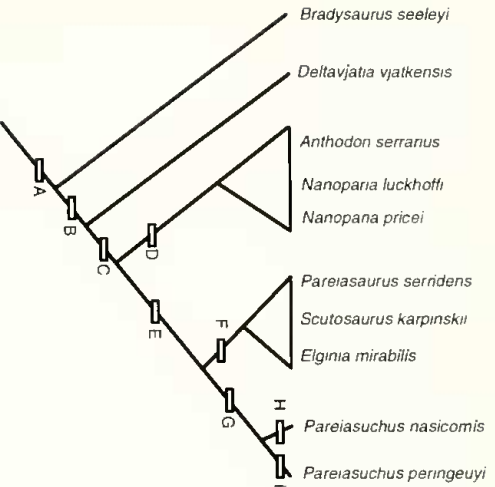
Anatomical considerations

The above description of *Pareiasuchus uasicornis* substantially modifies previous interpretations of the cranial anatomy. Boonstra (1934a) suggested that *Pareiasuchus uasicornis* (along with *P. peringueyi*) possessed a very depressed snout, a low braincase and supraoccipital pillar, and a quadrate that is much inclined anteroventrally. However, these all appear to be taphonomic artefacts, Boonstra having based his observations only on the holotype skull of *P. uasicornis*, SAM 3016. This skull has been compressed dorsoventrally, producing the flat snout, braincase, and supraoccipital. This crushing also displaced the dorsal ramus of the quadrate from its normal vertical position into an oblique position. Boonstra (1934a) also suggested that the maxilla of *P. uasicornis* was shallow, and that the maxilla-jugal contact was absent. However, none of the sutures is very clear on his specimen, whereas BPI 1/3653 clearly shows that the maxilla has an anterodorsal expansion and contacts the jugal. The sutures in the illustrations of Boonstra (1934a), which are all dotted and thus hypothetical, are also partly inaccurate. Apart from the anomalies already noted, the supernumerary element was assumed incorrectly to be absent, the parietals and supratemporal are much too narrow, and the postparietal is depicted as rectangular instead of U-shaped.

Because of lack of adequate descriptions, Gauthier *et al.* (1988b) misinterpreted the distribution of many characters in pareiasaurs. They asserted that pareiasaurs lacked both a maxilla-jugal contact and an enlarged foramen palatinum posterius (which they homologized with the diapsid suborbital foramen), and possessed a convex occipital condyle, a vomer that is narrower anteriorly and broader posteriorly, a postparietal which is occipital, and premaxillary teeth that are smaller than maxillary teeth. The present study of *Pareiasuchus uasicornis* reveals that the maxilla-jugal contact and enlarged foramen palatinum posterius are both present, and that the occipital condyle is concave, the vomer is broader anteriorly, the postparietal is exposed on the skull roof, and the premaxillary teeth are the largest in the tooth row. All other adequately known pareiasaurs are identical to *P. uasicornis* with respect to these characters (Lee, pers. obs.).

The supratemporal element in pareiasaurs has been identified usually as a 'tabular' (e.g. Haughton and Boonstra 1929a; Hartmann-Weinberg 1933; Boonstra 1934a; Bystrow 1957). However, its position on the skull roof, rather than on the occiput, and its lack of contact with the supraoccipital, suggest that it is a supratemporal. In diadectomorphs, and all basal amniotes which retain both a supratemporal and a tabular, the supratemporal has these relationships, whereas the tabular is occipital and contacts the supraoccipital. Furthermore, a phylogenetic analysis of parareptiles (Lee 1995) has revealed that the successive outgroups of pareiasaurs are turtles, lathanosuchids and procolophonoids: these taxa all lack a tabular but possess a large supratemporal. Hence, both topological similarity and phylogenetic continuity (character congruence) indicate that the large temporal element in pareiasaurs is a supratemporal, not a tabular.

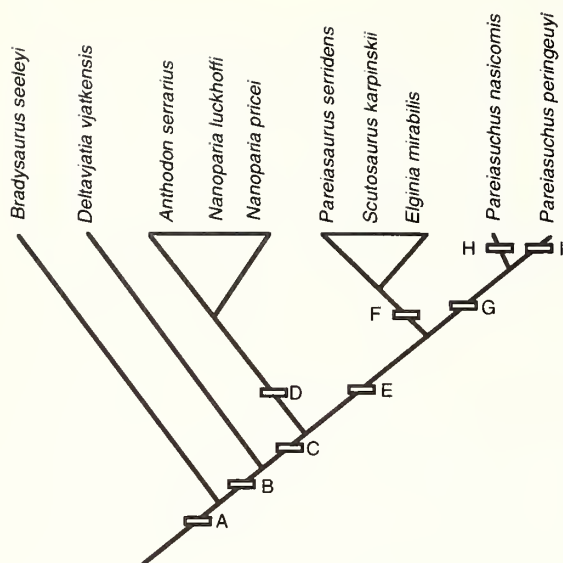
The identity of the 'supernumerary bone' between the supratemporal and the postparietal is also disputed. Wild (1985) called it a 'tabular', whilst Brink (1955), Walker (1973) and Maxwell (1991)



TEXT-FIG. 9. The phylogenetic relationships of *Pareasaurus nasicornis* to other well-known pareasaur taxa. Characters diagnosing the labelled groupings are discussed in the text. The position of turtles in this scheme is uncertain: as discussed in Lee (1996), they are either nested within pareasaur taxa (as part of Clade D), or are the sister group to pareasaur taxa (and thus are the sister group to Clade A).

interpreted it as a cervical osteoderm that had been incorporated into the cranium. There is a third possibility: that the bone is a neomorphic ossification. Critical developmental evidence is lacking; the homology of the supernumerary bone cannot be established unequivocally. It is not a persistent tabular, since the tabular has been lost in all the outgroups to pareasaur taxa. Furthermore, the supernumerary bone lies on the skull table, medial to the supratemporal, in a very different position from the tabular of other basal amniotes. There is thus neither phylogenetic continuity nor topographical similarity to suggest that the supernumerary bone in pareasaur taxa is a tabular (see above). However, it is difficult to choose between the two remaining possibilities. Many taxa (e.g. ceratopsians, ankylosaurs) incorporated osteoderms into the cranium, and in the dwarf pareasaur *Nanoparia luckhoffi*, an osteoderm has clearly been incorporated into the skull between the squamosal and the supratemporal (Broom 1936; Brink 1955). In all these cases, the osteoderms overlie the original cranial elements and are very superficial. The supernumerary bone in pareasaur taxa, however, appears to be integrated completely into the cranium, and the evidence for it being an osteoderm is less conclusive. Thus, the possibility remains of it being a neomorph – an entirely new ossification centre appearing between the postparietal and supratemporal. Intriguingly, in one skull of *Scutosaurus* (PIN 156/2), the supernumerary element appears to have fallen out from the back of the skull, which is otherwise complete. This suggests that it was less firmly attached than the other skull bones and supports (albeit weakly) the view that it represents a modified osteoderm.

The linear dimensions of Bp1 1/3653 are about three-quarters of those of the largest specimens of *P. nasicornis*: 301.6 (the type), GSP 475 and GSP CBT4. Bp1 1/3653 also differs from the latter skulls in some other features, all related to cranial ornament. The angular boss is a low rounded swelling, rather than a horn-like process. The bosses around the quadratojugal are also less prominent. The maxilla is smooth, rather than ornamented. In these respects, it is similar to other small skulls here assigned to *P. nasicornis*: SAM K6607 and GSP TN257. These differences are almost certainly ontogenetic: cranial ornament is more prominent in larger individuals of many taxa (Dodson 1975). In particular, the same differences are found in specimens which have been interpreted as juvenile and adult *Pareasuchus peringueyi* and *Scutosaurus karpinskii* (Lee 1994b). The lack of a bony separation between the fenestra ovalis and the foramen jugular anterius might also be the result of incomplete ossification in an immature animal. The open sutures in Bp1 1/3653 might also be a juvenile feature. Some sutures are also faintly visible on one of the other small skulls (SAM K6607) but are not visible on the other (GSP TN257), or on any of the large skulls. Sutures



TEXT-FIG. 9. The phylogenetic relationships of *Pareiasuchus nasicornis* to other well-known pareiasaurs. Characters diagnosing the labelled groupings are discussed in the text. The position of turtles in this scheme is uncertain: as discussed in Lee (1996), they are either nested within pareiasaurs (as part of Clade D), or are the sister group to pareiasaurs (and thus are the sister group to Clade A).

interpreted it as a cervical osteoderm that had been incorporated into the cranium. There is a third possibility: that the bone is a neomorphic ossification. Critical developmental evidence is lacking; the homology of the supernumerary bone cannot be established unequivocally. It is not a persistent tabular, since the tabular has been lost in all the outgroups to pareiasaurs. Furthermore, the supernumerary bone lies on the skull table, medial to the supratemporal, in a very different position from the tabular of other basal amniotes. There is thus neither phylogenetic continuity nor topographical similarity to suggest that the supernumerary bone in pareiasaurs is a tabular (see above). However, it is difficult to choose between the two remaining possibilities. Many taxa (e.g. ceratopsians, ankylosaurs) incorporated osteoderms into the cranium, and in the dwarf pareiasaur *Nanoparia luehkhoffi*, an osteoderm has clearly been incorporated into the skull between the squamosal and the supratemporal (Broom 1936; Brink 1955). In all these cases, the osteoderms overlie the original cranial elements and are very superficial. The supernumerary bone in pareiasaurs, however, appears to be integrated completely into the cranium, and the evidence for it being an osteoderm is less conclusive. Thus, the possibility remains of it being a neomorph – an entirely new ossification centre appearing between the postparietal and supratemporal. Intriguingly, in one skull of *Scutosaurus* (PIN 156/2), the supernumerary element appears to have fallen out from the back of the skull, which is otherwise complete. This suggests that it was less firmly attached than the other skull bones and supports (albeit weakly) the view that it represents a modified osteoderm.

The linear dimensions of BPI 1/3653 are about three-quarters of those of the largest specimens of *P. nasicornis*: 3016 (the type), GSP 475 and GSP CBT4. BPI 1/3653 also differs from the latter skulls in some other features, all related to cranial ornament. The angular boss is a low rounded swelling, rather than a horn-like process. The bosses around the quadratojugal are also less prominent. The maxilla is smooth, rather than ornamented. In these respects, it is similar to other small skulls here assigned to *P. nasicornis*: SAM K6607 and GSP TN257. These differences are almost certainly ontogenetic: cranial ornament is more prominent in larger individuals of many taxa (Dodson 1975). In particular, the same differences are found in specimens which have been interpreted as juvenile and adult *Pareiasuchus peringueyi* and *Scutosaurus karpinski* (Lee 1994b). The lack of a bony separation between the fenestra ovalis and the foramen jugular anterius might also be the result of incomplete ossification in an immature animal. The open sutures in BPI 1/3653 might also be a juvenile feature. Some sutures are also faintly visible on one of the other small skulls (SAM K6607) but are not visible on the other (GSP TN257), or on any of the large skulls. Sutures

are also clearer in smaller individuals of *Bradysaurus* (Broom 1924) and *Scutosaurus* (Lee 1994b). Finally, the fragmentary postcranial elements of this animal show one feature characteristic of juvenile reptiles: the neural arches and centra are separate (Kemp 1986).

Phylogenetic implications

The position of Pareiasuchus nasicornis within pareiasaurs. The information derived from this new specimen was included in a phylogenetic analysis which considered 128 osteological characters and all valid species of pareiasaurs, together with turtles, procolophonoids, lanthanosuchids, nyctiphuretids and nycteroleterids (Lee 1994b). A summary of the results is presented in Text-figure 9, which shows the systematic position of *P. nasicornis* relative to the better-known taxa of pareiasaurs. As discussed in the diagnosis of the genus *Pareiasuchus*, *Pareiasuchus nasicornis* and *Pareiasuchus peringueyi* are immediate relatives, based on the following synapomorphies: the narrow, distally projecting ent- and ectepicondyles; the greatly anterodorsally inclined iliac shaft; the flattened second and third sacral ribs; and the sharply bent femoral shaft. *Pareiasuchus* is related to other pareiasaurs which possess heavy cranial ornament, i.e. *Scutosaurus*, *Pareiasaurus*, *Elginia* and *Parasaurus*. The dwarf pareiasaurs (*Anthodon*) and the large, massively ossified forms (*Bradysaurus*) are very distantly related to this clade. Turtles might be part of the clade of dwarf pareiasaurs: a full discussion of this is presented elsewhere (Lee 1994b). The characters diagnosing the groupings in Text-figure 9 are listed below: they are the unambiguous (uniquely derived and unreversed) characters identified in the analysis just mentioned (Lee 1994b). For each character listed below, the derived state is listed first, while the primitive state (found in pareiasaurs outside the relevant clade, and in the nearest outgroups to pareiasaurs: lanthanosuchids, procolophonoids, nyctiphuretids, and nycteroleterids) follows in parentheses. These characters are discussed in detail and illustrated in Lee (1994b).

Clade A. All pareiasaurians. See Lee (1995).

Clade B. (1) humeral torsion 45° or less (torsion 60°); (2) osteoderms with a distinct central boss (osteoderms smooth); (3) basal tubera positioned anteriorly, mid-way between basiptyergoid processes and occipital condyle (basal tubera positioned closer to occipital condyle); (4) upper and lower marginal teeth with nine or more cusps (upper and lower marginal teeth with seven cusps); (5) cusps evenly spaced around tooth crown (cusps not evenly spaced – central or terminal three cusps much more close together than the cusps on the anterior and posterior margins); (6) 19 or fewer presacral vertebrae (20 or more presacrals); (7) cleithrum absent (cleithrum present in *Bradysaurus* and most of the outgroups, but also absent in derived procolophonoids).

Clade C. (1) dentary teeth with 12 or more cusps (dentary teeth with 11 or fewer cusps); (2) 20 or fewer caudal vertebrae (more than 20 caudals); (3) dermal armour covers entire dorsum (dermal armour restricted to dorsal midline in *Bradysaurus* and *Deltavjatia*, and absent in the outgroups); (4) limbs covered in conical bony studs (limbs without dermal armour).

Clade D. (1) scapula blade cylindrical (scapula blade flat and plate-like); (2) ulnar trochlea on humerus is a discrete tubercle (ulnar trochlear on humerus is a groove); (3) olecranon process reduced (olecranon process prominent in all other pareiasaurs, and in most related taxa, but convergently reduced in some procolophonoids); (4) trochanter major enlarged into a prominent tubercle (trochanter major present as a weak swelling in other pareiasaurs, absent in the other taxa); (5) trochanter major positioned very proximally, directly under capitellum (trochanter major positioned distal to capitellum in other pareiasaurs, absent in other taxa); (6) cnemial crest on tibia greatly reduced (cnemial crest is a prominent ridge); (7) osteoderms united over entire body (osteoderms separate).

Clade E. (1) lingual surface of dentary teeth with a distinct triangular ridge, widest near the base and tapering distally (lingual surface of dentary teeth smooth); (2) anterior expansion of blade of ilium greatly everted, being almost horizontal (blade of ilium slightly everted, or not at all); (3) osteoderms with highly irregular, rugose ridges radiating from the central boss (osteoderms without irregular, rugose ridges).

Clade F. (1) tubercle on ventral surface of basiptyergoid process (tubercle absent); (2) horn on maxilla, immediately posterior to external naris (horn absent).

Clade G. *Pareiasuchus*. See generic diagnosis.

Clade H. *Pareiasuchus peringueyi*. (1) Angular boss blunt (angular boss horn-like); (2) palatal ramus of the quadrate with large, posteriorly directed spine (spine absent).

Clade I. *Pareiasuchus nasicornis*. See specific diagnosis.

The position of pareiasaurs within Amniota. It has been proposed recently that pareiasaurs are the nearest relatives of turtles (Lee 1993, 1995). Alternative hypotheses are that the nearest relatives of turtles are captorhinids (Gaffney and Meylan 1988; Gauthier *et al.* 1988a, 1988b), or procolophonoids (Reisz and Laurin 1991; Laurin and Reisz 1993, 1995). Gardiner's (1982) radical proposal that dicynodonts are the nearest relatives of turtles has not found any acceptance (e.g. Gay 1987; King 1988; Lee 1995), and Gardiner himself no longer holds this view (see Gardiner 1993). A fuller treatment of turtle relationships is presented elsewhere (Lee 1995). However, it should be emphasized that all these discussions have been hampered by a lack of accurate, detailed descriptions of pareiasaur anatomy.

The present excellent specimen sheds light on this problem in clearly showing several proposed pareiasaur-turtle synapomorphies (some of which have been inadequately described in pareiasaurs until now). It also demonstrates the presence in pareiasaurs of traits previously asserted to be restricted either to procolophonoids and turtles, or to captorhinids and turtles. This new information thus strengthens arguments for a pareiasaur-turtle clade and weakens alternative suggestions. *Pareiasuchus nasicornis* possesses the following traits, proposed to be pareiasaur-turtle synapomorphies (Lee 1995): a large foramen palatinum posterius; a medially positioned choana; a blunt cultriform process; a horizontal transverse flange of the pterygoid; opisthotic-squamosal suture; a long lateral flange of the exoccipital; and a narrow supraoccipital with a long sagittal suture with the skull table. These are present in other adequately known pareiasaurs (Lee, pers. obs.).

The described specimen also casts doubt over many proposed procolophonoid-turtle synapomorphies. BPI 1/3653 shows that *Pareiasuchus nasicornis*, like other adequately known pareiasaurs, has a short cultriform process, a wide antorbital buttress formed by the prefrontal and palatine, an anterior expansion of the maxilla, an occipital flange of the squamosal, an enlarged quadratojugal, a notched anterior end of the splenial, and a medially enclosed adductor fossa. These traits have recently been proposed as procolophonoid-turtle synapomorphies (Reisz and Laurin 1991; Laurin and Reisz 1993, 1995). Discovery of them in pareiasaurs indicates that they diagnose a more inclusive grouping. A further proposed procolophonoid-turtle synapomorphy, the large basal tubera on the basioccipital, is not found in primitive turtles such as *Proganochelys*. Furthermore, as shown in the above description, *P. nasicornis*, like all pareiasaurs, also has basal tubera. These are formed mainly by the basisphenoid, but their posterior portions are formed by the basioccipital.

The above description also has relevance to the proposed captorhinid-turtle clade. BPI 1/3653, like all pareiasaurs (Lee, pers. obs.), has a foramen-orbitonasale, and lacks a tabular: these traits have previously been interpreted as the most compelling captorhinid-turtle synapomorphies (Gaffney and Meylan 1988). Lack of adequate published information on pareiasaur anatomy has caused previous workers to misinterpret the distribution of these characters.

Some previous descriptions of pareiasaurs have suggested incorrectly that, with respect to the above characters, some pareiasaurs differ from *P. nasicornis*. Haughton and Boonstra (1929b) depicted a tapering, rather than forked, splenial in some pareiasaurs (e.g. *Anthodon serrarius*, *Propappus omocratus*). However, examination of the relevant specimens reveals that in each case the dorsal prong of the fork in the splenial has been lost through crude preparation. All adequately prepared pareiasaur material shows the forked splenial (Lee, pers. obs.). Ivachnenko (1987) has depicted some individuals of *Scutosaurus* with a long cultriform process: examination of the material of this taxon, including the specimens used in his reconstructions, reveals the cultriform process to be short. Similarly, a few illustrations of *Proganochelys* in Gaffney (1990) depict a long

cultriform process; however, most depict a short, blunt process, which is the actual condition (Gaffney, pers. comm. 1995).

Thus, the preceding description of the excellently preserved skull helps confirm many pareiasaur-turtle synapomorphies, and simultaneously casts doubt over many of the synapomorphies proposed for alternative groupings. The problem of whether turtles are related to procolophonoids or to pareiasaurs is discussed more fully elsewhere (Lee 1994b, 1995) and it was found that only two of the 17 procolophonoid-turtle synapomorphies recently proposed by Laurin and Reisz (1995) appear to be valid, while over 20 derived characters unite pareiasaurs and turtles.

FUNCTIONAL MORPHOLOGY

The skull of *Pareiasuchus nasicornis* is heavily ossified, solid, and completely akinetic: the braincase is sutured to the skull roof via the supraoccipital, the paroccipital process, and presumably the pleurospenoid. The palate is held firmly in place, not only by the usual contacts with the quadrate and above the alveolar ridge, but also via the fused basicranial articulation and the robust antorbital buttress.

The pareiasaur skull, as exemplified by *P. nasicornis*, clearly reflects herbivorous habits, despite two previous suggestions to the contrary. Hartmann-Weinberg (1937) suggested that pareiasaurs were aquatic predators that fed on amphibian larvae, based largely on the co-occurrence of the two taxa in the same deposits in Russia. Case (1926) suggested that they consumed floating algal mats, based on their 'weak' dentition. However, these interpretations of pareiasaurs as aquatic feeders are not supported by their postcranial morphology, which exhibit no indications of aquatic habits (e.g. Lee 1994a). Conversely, pareiasaurs possessed many other features well-known to be characteristic of terrestrial herbivores.

The 'weak' dentition is, in fact, quite typical of herbivores. The teeth are labiolingually compressed and expanded anteroposteriorly, bearing numerous large cusps arranged in a single row around the edge. Such teeth are characteristic of herbivorous terrestrial reptiles, such as numerous groups of ornithischian dinosaurs (e.g. stegosaurs, fabrosaurids), synapsids (e.g. caseids) and squamates (e.g. iguanids). In extant forms, they have been shown to be correlated with herbivory (Hotton 1955; Montanucci 1968). The deep tooth sockets in pareiasaurs allowed replacement teeth to reach a large size before the old tooth was shed, allowing rapid replacement of teeth and thus, reducing the number of gaps in the cutting edge (Edmund 1969; Throckmorton 1976). The anteroposteriorly expanded teeth, lack of interdental spaces, and isodont dentition combine to form an uninterrupted, even cutting edge, very different from the puncturing dentition typical of most basal amniotes, which were insectivorous (Carroll 1964, 1982). Such a cutting edge is characteristic of herbivores that employ a cropping action (Montanucci 1968; Norman 1984; Galton 1986). This cropping action does not require contact between the upper and lower marginal teeth: rather, the upper and lower tooth rows slide closely past one another in a scissor-like action (Throckmorton 1976). Accordingly, the teeth of pareiasaurs never show any wear facets or other signs of attrition (tooth-to-tooth wear; Osborn and Lumsden 1978). The reduction of the transverse flange (see above) is also correlated with herbivory. This structure represents the origin of the anterior pterygoideus muscle (part of the internal adductors). This muscle, which pulls upwards and forwards, acts most effectively (perpendicular to the long axis of the lower jaw) when the jaws are widely open, and is most important in the kinetic-inertial feeding systems of carnivores (e.g. Olson 1961). It also serves to guide the lower jaw and helps prevent dislocation when the jaws are closed against struggling prey. In reptilian herbivores, which have a static feeding system (Olson 1961), the anterior pterygoideus is less important, and problems with struggling prey do not occur, and thus the transverse flange of the pterygoid is reduced (e.g. King *et al.* 1989; King 1990). The coronoid process is also reduced, compared with the condition in most other 'parareptiles' such as nyctiphruetids, procolophonoids and turtles. The medial external adductors which insert on the coronoid process pull backwards and upwards on the process, and thus function most effectively

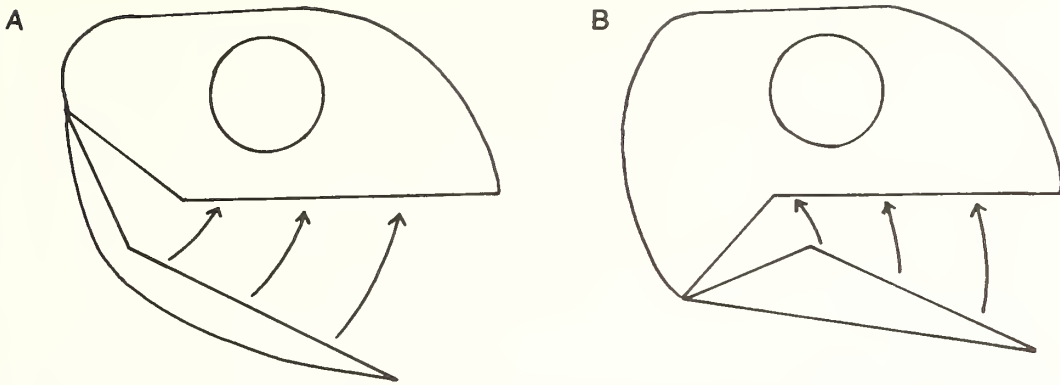
when the coronoid process is oriented perpendicular to the line of muscle action (i.e. when the jaws are wide open). The coronoid process, like the transverse flange of the pterygoid, is emphasized in the kinetic-inertial jaws of carnivores, and is reduced in herbivores (Janis 1995). The pareiasaurian mandible is very heavy. The anterior position of the jaw articulation means that the lower jaw of pareiasaurs is rather short. Given the weakness of the pterygoideus complex, the heaviness of the mandible, and the shortness of the lower jaw, the gape of pareiasaurs was undoubtedly rather narrow, and the jaw movements slow. All these features are consistent with herbivory.

As in many herbivores, the jaw articulation is positioned well below the tooth row (Norman 1984; Galton 1986). This arrangement allows for simultaneous occlusion of cheek teeth (Greaves 1995; Janis 1995). Also, Davis (1964) has demonstrated that, when the jaw articulation is raised above the level of the tooth row, an anteriorly directed shearing force is generated during occlusion, even if the muscles act perpendicular to the long axis of the lower jaw (Text-fig. 10A). Using the same model, it can be shown that if the articulation is positioned *below* the tooth row, as in *Scutosaurus*, a posteriorly directed force is generated during occlusion (Text-fig. 10B). The posterior forces are most pronounced near the rear of the tooth row, for geometric reasons (Text-fig. 10B). Such shearing forces have been demonstrated to facilitate cropping of tough plant matter (Throckmorton 1976).

Although pareiasaurs were clearly herbivores, there are no indications of cheeks, no complex tooth batteries or other elaborate masticatory adaptations. Oral processing of food appears to have been limited to cropping bits of vegetation before swallowing. Such feeding behaviour is characteristic of extant iguanid squamates (Throckmorton 1976), which have dentition very similar to that of pareiasaurs. In pareiasaurs, the cropping action would have been facilitated by propalinal movements. Given their large size and broad snouts (see Jarman 1974; van Soest 1982; Janis and Erhardt 1988), pareiasaurs were probably not very selective feeders, ingesting large amounts of low-quality food. There is no evidence of gastralgia, despite the fact that pareiasaur skeletons are commonly found articulated (Kitching 1977). Pareiasaurs therefore needed to process large quantities of low-grade food, but lacked the efficient equipment (dentition, gastralgia) to break it down mechanically. They presumably coped by storing large amounts in the fermentation chambers for long periods, resulting in their large, bulky bodies.

The function of the distinctive cheek flanges of pareiasaurs has never been properly discussed. Among extant taxa, edentate mammals have a projection in this area, which serves as an origin for muscles which move the lower jaws laterally during mastication (Naples 1982). However, a transversely oriented power stroke is known only in mammals and certain ornithomimid dinosaurs, and in each case is accompanied by complex jaw adaptations (Weishampel 1984). The saddle-shaped jaw articulation, and shearing dentition of pareiasaurs obviously combined to preclude lateral grinding jaw movements (see King *et al.* 1989 for similar arguments pertaining to dicynodonts). Hence, the possibility that the pareiasaur cheek flanges served a similar function can be discounted. Pareiasaurs appear to have been very slow-moving animals, were too large to remain cryptic, and possessed no obvious offensive weapons. They appear to have adopted passive anti-predator defences: large size, blunt protective bosses over delicate organs such as the eyes and nostrils, and dermal armour over the body and limbs (Gow 1977; Lee 1994a). Interpreting the cheeks as defensive structures is therefore consistent with information derived from other areas of the body. The rows of large bosses on the edge of these cheek flanges are also consistent with this interpretation. Nopsca (1928) long ago remarked that the cheeks of pareiasaurs are very similar to those of ankylosaurs. Ankylosaurs and pareiasaurs both possessed strong defensive structures in other parts of the body, and the cheek flanges in these taxa may have helped protect the vulnerable throat region.

The role of the ventrally directed boss on the mandible also remains uncertain. It is clearly partly an allometric feature. It is a small, rounded boss in young pareiasaurs (such as this individual of *Pareiasuchus nascornis*) and dwarf forms (such as *Nanoparia pricei* BPI 1/7), but is a prominent conical spike in all adults of large pareiasaurs. Similarly, very large individuals of the procolophonoid *Procolophon* possess a weak rugosity in this area, but this feature is absent in



TEXT-FIG. 10. Illustration of how simple elevation or depression of the jaw articulation results in shearing movements during occlusion, even in the absence of anteroposterior sliding (propalinal) movements at the jaw articulation. Arrow shafts are concentric to the jaw articulation, and represent the trajectory of the lower jaw during occlusion. A, an elevated jaw articulation results in a forward shearing of the lower jaw during occlusion. B, a depressed jaw articulation, as found in *Scutosaurus* and other pareiasaurs, results in a backwards shearing of the lower jaw during occlusion.

smaller individuals. Although obviously partly a correlate of large size, the observation that the angular boss was retained in all lineages of large pareiasaurs suggests some functional significance, but no clear explanation is apparent. Perhaps, like the cheek flanges, it helped to protect the vulnerable throat region. The only other amniotes with a boss in this region are entelodont mammals. However, the only comprehensive study of their functional cranial anatomy (Joeckel 1990) did not speculate on the function of the mandibular boss. Furthermore, the rest of the cranial architecture in entelodonts is so different from that of pareiasaurs that using these animals as analogues for one another would be very unwise.

Acknowledgements. ML gratefully acknowledges financial assistance from The Association of Commonwealth Universities, The British Council, The Cambridge Philosophical Society, The Balfour Fund, Queens' College (Cambridge), and the Australian Research Council, and thanks Rick Shine and colleagues for use of laboratory and office facilities and Malcom Ricketts for photographic assistance during the final stages of preparation of this manuscript. We are indebted to the following people for hospitality and access to specimens during museum visits: Gillian King, Madel Joubert, Clive Booth and Roger Smith (South African Museum), Oleg Lebedev, Michael Ivachenko and Nick Kalandadze (Palaeontological Institute, Moscow), and Andre Keyser and Francois Durand (Geological Survey, Pretoria).

REFERENCES

- ARAÚJO, D. C. F. 1984. Sistemática e taxonomia dos pareiasauros: historico e perspectivas atuais. *Pesquisas*, **16**, 227–249.
- 1989. Estudo do material Sul-Americano de Pareiasauroidea. VI. Descrição do esqueleto axial de *Pareiasaurus americanus* Araújo, 1985. *Anais do Academie Brasileira Ciências*, **61**, 295–309.
- BOONSTRA, L. D. 1929a. Pareiasaurian studies. Part III. On the pareiasaurian manus. *Annals of the South African Museum*, **28**, 97–112.
- 1929b. Pareiasaurian studies. Part IV. On the pareiasaurian pes. *Annals of the South African Museum*, **28**, 113–122.
- 1932. Pareiasaurian studies. Part VIII. The osteology and myology of the locomotor apparatus. Part B. Fore limb. *Annals of the South African Museum*, **28**, 436–503.
- 1934a. Pareiasaurian studies. Part IX. The cranial osteology. *Annals of the South African Museum*, **31**, 1–38.
- 1934b. Pareiasaurian studies. Part X. The dermal armour. *Annals of the South African Museum*, **31**, 39–48.

- 1934c. Pareiasaurian studies. Part XI. The vertebral column and ribs. *Annals of the South African Museum*, **31**, 49–66.
- BRINK, A. S. 1955. On *Nanoparia*. *Palaeontologia Africana*, **3**, 57–63.
- BROOM, R. 1909. An attempt to determine the horizons of the fossil vertebrates of the Karroo. *Annals of the South African Museum*, **7**, 285–289.
- 1924. On some points in the structure of the pareiasaurian skull. *Proceedings of the Zoological Society of London*, **1924**, 499–508.
- 1936. On some new genera and species of Karroo fossil reptiles, with notes on some others. *Annals of the Transvaal Museum*, **18**, 349–386.
- 1940. On some new genera and species of fossil reptiles from the Karroo beds of Graaf-Reinet. *Annals of the Transvaal Museum*, **20**, 157–192.
- and HAUGHTON, S. H. 1913. On the skeleton of a new pareiasaurian (*Pareiasuchus peringueyi*, g. et. sp. nov.). *Annals of the South African Museum*, **12**, 17–25.
- BRYANT, H. N. and RUSSELL, A. P. 1992. The role of phylogenetic analysis in the inference of unpreserved attributes of extinct taxa. *Philosophical Transactions of the Royal Society of London, Series B*, **337**, 405–418.
- BYSTROW, A. P. 1957. [The pareiasaur skull.] *Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR*, **68**, 3–18. [In Russian].
- CARROLL, R. L. 1964. The earliest reptiles. *Zoological Journal of the Linnean Society*, **45**, 61–83.
- 1982. The early evolution of reptiles. *Annual Review of Ecology and Systematics*, **13**, 87–109.
- CASE, E. C. 1926. Environment of tetrapod life in the late Paleozoic of regions other than North America. *Publication of the Carnegie Institute of Washington*, **375**, 1–211.
- DAVIS, D. D. 1964. The giant panda: a morphological study of evolutionary mechanisms. *Fieldiana, Zoology Memoir*, **3**, 1–339.
- DODSON, P. 1975. Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Zoology*, **24**, 37–54.
- DRYSDALL, A. R. and KITCHING, J. W. 1963. A re-examination of the Karroo succession and fossil localities of part of the Upper Luangwa Valley. *Memoir of the Geological Survey of Northern Rhodesia*, **1**, 1–62.
- EDMUND, A. G. 1969. Dentition. 117–200. In GANS, C., BELLAIRS, A. d'A., PARSONS, T. S. (eds). *Biology of the Reptilia*. Volume 1. Academic Press, London, 373 pp.
- GAFENEY, E. S. 1979. Comparative cranial morphology of Recent and fossil turtles. *Bulletin of the American Museum of Natural History*, **164**, 65–376.
- 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, **194**, 1–263.
- and MEYLAND, P. A. 1988. A phylogeny of turtles. 157–219. In BENTON, M. J. (ed.). *The phylogeny and classification of tetrapods*. Clarendon Press, Oxford, 377 pp.
- GALTON, P. M. 1986. Herbivorous adaptations of Late Triassic and Early Jurassic dinosaurs. 203–221. In PADIAN, K. (ed.). *The beginning of the age of dinosaurs*. Cambridge University Press, Cambridge, 378 pp.
- GARDINER, B. G. 1982. Tetrapod classification. *Zoological Society of the Linnean Society*, **74**, 207–232.
- 1993. Haematothermia: warm-blooded amniotes. *Cladistics*, **9**, 368–395.
- GAUTHIER, J. A., KLUGE, A. G. and ROWE, T. 1988a. Amniote phylogeny and the importance of fossils. *Cladistics*, **4**, 105–209.
- — — 1988b. The early evolution of the Amniota. 103–155. In BENTON, M. J. (ed.). *The phylogeny and classification of the tetrapods*. Clarendon Press, Oxford, 377 pp.
- GAY, S. A. 1987. A dicynodont fauna from the Permian of Tanzania. Unpublished Ph.D dissertation, University of Cambridge, U.K.
- GOW, C. E. 1977. *Owenetta* in perspective. *Palaeontologia Africana*, **20**, 115–118.
- GREAVES, W. S. 1995. Functional predictions from theoretical models of the skull and jaws in reptiles and mammals. 99–115. In THOMASON, J. J. (ed.). *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge, 277 pp.
- HAEKEL, E. 1866. *Generelle Morphologie der Organismen*. Reimes, Berlin.
- HARTMANN-WEINBERG, A. 1933. Die Evolution der Pareiasauriden. *Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR*, **3**, 3–66.
- 1937. Pareiasauriden als leitfossilien. *Problemy paleologii*, **2/3**, 649–712.
- HAUGHTON, S. H. and BOONSTRA, L. D. 1929a. Pareiasaurian studies. Part I. An attempt at a classification of the Pareiasauria based on skull features. *Annals of the South African Museum*, **28**, 79–87.
- — — 1929b. Pareiasaurian studies. Part V. On the pareiasaurian mandible. *Annals of the South African Museum*, **28**, 261–289.

- . 1930. Pareiasaurian studies. Part VI. The osteology and mycology of the locomotor apparatus. A. Hind limb. *Annals of the South African Museum*, **28**, 297–367.
- HEATON, M. J. 1979. The cranial anatomy of primitive captorhinid reptiles from the Pennsylvanian and Permian of Oklahoma and Texas. *Bulletin of the Oklahoma Geological Survey*, **127**, 1–84.
- HOTTON, N., III. 1955. A survey of adaptive relationships of dentition to diet in the North American Iguanidae. *American Midland Naturalist*, **53**, 88–114.
- HUENE, F. von 1944. Pareiasaurierreste aus dem Ruhu-Gebiet. *Paläontologische Zeitschrift*, **23C**, 386–410.
- IVACHENKO, M. F. 1987. [Permian parareptiles of the USSR.] *Trudy Paleontologicheskogo Instituta, Akademiia Nauk SSSR*, **223**, 3–16. [In Russian].
- JANIS C. M. 1995. Correlations between craniodental morphology and feeding behavior in ungulates: reciprocal illumination between living and fossil taxa. 76–98. In THOMASON, J. J. (ed.). *Functional morphology in vertebrate paleontology*. Cambridge University Press, Cambridge, 277 pp.
- and ERHARDT, D. 1988. Correlation of relative muzzle width and relative incisor width with dietary preference in ungulates. *Zoological Journal of the Linnean Society*, **92**, 267–284.
- JARMAN, P. J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour*, **58**, 215–267.
- JOECKEL, R. M. 1990. A functional interpretation of the masticatory system and paleoecology of entelodonts. *Paleobiology*, **16**, 459–482.
- KEMP, T. S. 1986. The skeleton of a bauriid therocephalian therapsid from the Lower Triassic (*Lystrosaurus* zone) of South Africa. *Journal of Vertebrate Paleontology*, **6**, 215–232.
- KEYSER, A. W. and SMITH, R. M. H. 1978. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Annals of the Geological Survey of South Africa*, **12**, 1–35.
- KING, G. M. 1988. *Anomodontia. Handbuch der Paläoherpetologie. Teil 17C*. Gustav Fischer Verlag, Stuttgart, 174 pp.
- . 1990. *The dicynodonts: a study in palaeobiology*. Chapman and Hall, London, 233 pp.
- OELOFSEN, B. W., and RUBIDGE, B. S. 1989. The evolution of the dicynodont feeding system. *Zoological Journal of the Linnean Society*, **96**, 185–211.
- KITCHING, J. W. 1963. The fossil localities and mammal-like reptiles of the Upper Luangwa Valley, Northern Rhodesia. *South African Journal of Science*, **59**, 259–264.
- . 1970. A short review of the Beaufort zoning in South Africa. 309–312. In HAUGHTON, S. H. (ed.). *I.U.G.S. Second Symposium on Gondwana Stratigraphy and Palaeontology*. C.S.I.R., Pretoria, 689 pp.
- and 1977. Distribution of the Karroo vertebrate fauna. *Memoir of the Bernard Price Institute for Palaeontological Research, University of Witwatersrand (Johannesburg)*, **1**, 1–131.
- KUHN, O. 1969. *Cotylosauria. Handbuch der Paläoherpetologie. Teil 6*. Gustav Fischer Verlag, Stuttgart, 89 pp.
- LAURENTI, J. N. 1768. *Specimen medicum, exhibens synopsis Reptilium emendatum, cum experimentalis circa Venena*. Vienna, 217 pp.
- LAURIN, M. and REISZ, R. R. 1993. The origin of turtles. *Journal of Vertebrate Paleontology*, **13**, 46A.
- . 1995. A reevaluation of early amniote phylogeny. *Zoological Journal of the Linnean Society*, **113**, 165–223.
- LEE, M. S. Y. 1993. The origin of the turtle body plan: bridging a famous morphological gap. *Science*, **261**, 1716–1720.
- . 1994a. The turtle's long lost relatives. *Natural History*, **103** (6), 63–65.
- . 1994b. Evolutionary morphology of pareiasaurs. Unpublished Ph.D Dissertation, University of Cambridge, U.K.
- . 1995. Historical burden in systematics and the interrelationships of parareptiles. *Biological Reviews*, **70**, 459–547.
- in press. A taxonomic revision of pareiasaurs: implications for Permian terrestrial palaeoecology. *Modern Geology*.
- MAXWELL, W. D. 1991. The pareiasaur *Elginia* from Elgin, north-east Scotland, and the Late Permian extinction event. Unpublished Ph.D Thesis, Queen's University, Belfast.
- MONTANUCCI, R. R. 1968. Comparative dentition in four iguanid lizards. *Herpetologica*, **24**, 305–315.
- NAPLES, V. L. 1982. Cranial osteology and function in tree sloths, *Bradypus* and *Choloepus*. *American Museum Novitates*, **2739**, 1–41.
- NEWTON, E. T. 1893. On some new reptiles from the Elgin sandstones. *Philosophical Transactions of the Royal Society of London, Series B*, **184**, 473–489.
- NOPCSA, F. 1928. Palaeontological notes on reptiles. *Geologica Hungarica*, **1**, 1–84.
- NORMAN, D. B. 1984. On the cranial morphology and evolution of ornithomimid dinosaurs. 521–547. In FERGUSON, M. W. (ed.). *The structure, development and evolution of reptiles*. Academic Press, London, 697 pp.